Monogamy in the bat-eared fox, *Otocyon megalotis*

by

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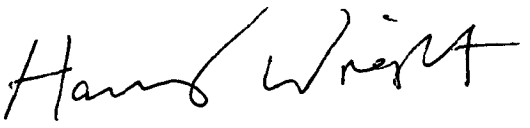
Declaration

Data presented in chapter 6 are the result of collaboration between myself and Melissa Gray of the Univesity of California Los Angeles. Melissa Gray was solely responsible for genotyping bat-eared fox tissue samples (the laboratory work), but the analysis and interpretation of results were performed jointly.

All other data presented in the thesis were collected and analysed by me alone. No data presented in this thesis have yet been published, or previously presented for a different degree.



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Summary

Mammalian monogamy is puzzling from and evolutionary perspective because it is unclear why males, which have the potential to father a great many offspring, should choose to associate with only one female. This project investigated the behaviour of a socially monogamous (pair-living) population of bat-eared foxes in Laikipia, Northern Kenya, and had two principal aims. The first aim was to identify the selective forces that operate to maintain social monogamy in the study population. The second aim was to determine whether bat-eared foxes mate exclusively with their social partners (i.e. if they are genetically as well as socially monogamous).

Chapter 1 summarizes by background to the research: Broadly speaking, theories advanced to explain the evolution of monogamy fall into two categories; those that proposing that monogamy occurs when male assistance is required for successful reproduction, and those that proposing that aspects of female spatial and/or temporal distribution make it impossible for even the most competitive males to gain more than one mate.

Chapter 2 describes the study site and general methods employed.

Chapter 3 examines whether a requirement for paternal care maintains social monogamy by investigating the parental roles of males and females: I found that females invest very heavily in reproduction, feeding at close to maximum rate throughout lactation and suffering increased mortality rates during this period. Consistent with previous studies of the species, I found that males are heavily involved in the rearing of young, spending significantly more time than females close to breeding dens, and contributing to all aspects of cub care. The importance of male care was revealed by the fact that, after statistically controlling for the confounding effects of territory quality, the male den attendance was significantly associated with cub survival.

Chapter 4 investigates factors other than the requirement for male care that may prevent males from achieving polygynous status: Social monogamy was not enforced because males were incapable of defending sufficient resources to support more than one female, as some male territories contained sufficient food to support two or more females. I found, however, that because females occupied largely exclusive ranges and had synchronized fertile periods, it was probably impossible for even the most competitive males to successfully defend more than one fertile female.

Chapter 5 investigates the mating tactics of bat-eared foxes by comparing their behaviour during and outside the mating season: Neither male nor female foxes increased their home range sizes during the mating season, demonstrating that they do not roam widely in search of extra-pair mates. Time-budget data suggest that this may be because bat-eared foxes have little time available to engage in activities other than foraging. The behaviour of mated partners wass highly coordinated, particularly during the mating season, and the close proximity of mated partners did not reduce their feeding rate.

Chapter 6 uses DNA microsatellite analyses to establish the paternity of bat-eared fox cubs: We found that for the vast majority of cubs (42 of 44) social fathers were most likely to be their true fathers. These data demonstrate a high level of genetic monogamy in the study population.

Chapter 7 summarizes data from the thesis: I conclude that, although male care enhances offspring survival, there are circumstances under which males may gain from polygyny. Males are probably unable to attain polygynous status, however, because the spatial and temporal distribution of females, combined with intense competition for mates makes it impossible for them to defend more than one mate. Consistent with observations of occasional polygynous breeding from other bat-eared fox populations, I conclude that polygyny could only a viable male strategy if compliant females were willing to co-ordinated their behaviour. I argue that the high levels of genetic monogamy observed are probably consequence of the species insectivorous diet, which leaves individuals with little time to engage in activities other than foraging, and makes it easy for males to guard their own partners.

Chapter 1

Introduction

1.1 Background to research

1.1.1 The evolution of mating systems

The vast array of social and reproductive systems exhibited by animals represent a significant and captivating challenge to evolutionary biologists. Why do dik-diks live in monogamous pairs, chimpanzees live in multi-male multi-female groups and ungulates like the Uganda Kob mate in promiscuous leks? Over the last 30 years biologists have, through theoretical and long-term field studies, sought to understand how natural selection has produced these vastly different social systems (e.g.Orians 1969, Emlen & Oring 1977, Clutton-Brock 1989).

A significant advance in our understanding of animal social behaviour stemmed from the realisation that the reproductive rates of males and females are often governed by different factors (Bateman 1948, Trivers 1972, Goss-Custard *et al.* 1972). In most taxa, and in the majority of species of mammal, females invest more time and energy in reproduction than males (Orians 1969, Trivers 1972). Under these circumstances males are able to father offspring at a greater rate than females can produce them, and at any one time the number of males capable of reproducing is higher than the number of

females capable of doing so (the ratio of which was defined by Emlen & Oring (1977) as the 'operational sex ratio', or OSR).

Males and females distribute themselves in the way that best suits their reproductive interests, given their ecological strategies and the distribution of essential resources (Rubenstien & Wrangham 1986). Because female mammals tend not to rely on paternal care, their spatial distribution is determined primarily by the abundance and distribution of food supplies (Jarman 1974, Clutton-Brock & Harvey 1978, Davies 1991, Sterck *et al.* 1997), but also mediated by other factors, including predation pressure and the costs of social living (Clutton-Brock 1989). Male reproductive success, on the other hand, is usually limited by the number of females that they can mate with (Trivers 1972). In line with this males often appear to compete to map their distribution onto those of the females, in an attempt to maximise the number of females they can fertilize (e.g. Charles-Dominique 1977, Sandell 1989).

The ability of males to monopolize fertile females depends crucially on the distribution of receptive females in time as well as space (Emlen & Oring 1977). When females are widely distributed in space and their oestrous periods are highly synchronized, it may be difficult or impossible for males to defend more than one receptive female. Conversely, when females are spatially clumped and their receptive periods are not synchronized, males have the greatest opportunity to monopolize access to them (Eberle & Kappeler 2002). In a sense then, many mating systems may represent male mate guarding

strategies adapted to both the spatial and temporal distribution of fertile females (Clutton-Brock 1989).

It is now widely recognized that conflicts of interest exist within almost all social relationships (Clutton-Brock 1989, Davies 1992). Males and females from the same social group may disagree about whom they mate with, and the relative amount of care they provide for offspring (Davies 1985). Because of this, Davies (1992) argues that mating systems should be viewed as outcomes of decisions made by individuals, each selected to maximize their own reproductive success.

Numerous field studies have demonstrated significant variation in social behaviour within and between populations of the same species (e.g. Woodroffe & Macdonald 1993, reviewed in Lott 1991). This intra-specific variation is apparently a consequence of the adaptive adjustment of male and female behaviour to differences in social and ecological environment (Crook & Goss-Custard 1972, Kruuk 1975, Clutton-Brock 1989, Balshine-Earn 1996).

1.1.2 What is monogamy?

Monogamy has been defined by Wittenberger & Tilson (1980) as 'a prolonged association and essentially exclusive mating relationship between one male and one female' (after Lack 1968, Kleiman 1977, Selander 1972, Wilson 1975, Wittenberger 1979). Their term 'prolonged association' implies that an exclusive social bond exists

between a 'mated pair' for the duration of at least one breeding event, and the term 'essentially exclusive mating relationship' implies that 'occasional matings outside the pair bond do not negate the existence of monogamy'. Wickler & Seibt (1983, p34) expanded on this, suggesting that it is helpful to make a distinction between 'social monogamy' (living with one partner) and 'genetic monogamy' (mating exclusively with one partner), and recognize that the two are not necessarily synonymous (section 1.1.4).

1.1.3 Why is monogamy puzzling?

Social monogamy is one of the most puzzling of mammalian mating systems because it is unclear what limits males to associating with a single female (Clutton-Brock 1989, Komers & Brotherton 1997). Because female mammals are committed to lengthy periods of gestation and lactation, males have little opportunity to become involved in the care of offspring (Orians 1969), and every opportunity to desert females (after mating) and search for new mates (Trivers 1972). In light of this, it is not surprising that fewer than 5 % of mammalian species are monogamous (Kleinman 1977). This contrasts sharply with the situation in birds, where social monogamy is the predominant mating system (Lack 1968).

Numerous hypotheses have been put forward to explain the evolution of mammalian monogamy (Gubernick 1994). These hypotheses have tended to make the distinction between obligate and facultative monogamy (after Kleiman 1977).

Obligate monogamy is thought to have evolved in species where male parental care is essential for offspring survival (Kleiman 1977, Wittenberger & Tilson 1980, Clutton-Brock 1989, Gubernick *et al.* 1993, Gowaty 1996), and constrains males to necessarily breed in monogamous pairs. Where male care is essential for successful breeding the operational sex ratio may approach parity (Clutton-Brock 1991), and under certain circumstances (for example if the population sex ratio is female biased) females may compete for access to male care (Davies 1992).

Facultative monogamy, on the other hand, was thought to have evolved when females are solitary and too highly dispersed to make polygyny possible (-the 'over-dispersion hypothesis' Emlen & Oring 1977, Wickler & Seibt 1983, Cockburn 1988). Some authors have related facultative monogamy to the inability of males to defend the resources required by more than one female (Murray 1984, Gosling 1986), and most assume that males would mate polygynously if higher female densities made monopolization of multiple females possible (Kleiman & Malcolm 1981, Barlow 1988).

The validity of the distinction between obligate and facultative monogamy has been questioned by field studies suggesting that obligate monogamy can evolve in the absence of paternal care (e.g. the dik-dik, Komers 1996), and that monogamous species exhibiting paternal care are occasionally polygynous (e.g. the red fox, Macdonald 1980; aardwolf, Richardson 1986). Komers (1996) suggests that the terms facultative and obligate monogamy should be redefined to solely describe the flexibility of monogamous mating systems, without implications about the presence or absence of paternal care.

The relative importance of the requirement for male care and the constraints imposed by female dispersion as factors favouring the evolution of mammalian social monogamy have recently been investigated in a comparative study by Komers & Brotherton (1997). They found that monogamy has evolved significantly more often in the absence of paternal care than in its presence, and that monogamy was most likely to evolve where females occupied small (rather than large) exclusive ranges. Komers & Brotherton (1997) conclude that exclusive defence of a single female must sometimes be advantageous to males. Studies on dik diks (Brotherton & Manser 1997) and elephant shrews (FitzGibbon 1997) support the idea that social monogamy can evolve solely as a mate guarding strategy.

It is clear that males of some species of monogamous mammal exhibit highly developed forms of parental care (Runcie 2000, Gubernick *et al.* 1993), whereas others provide no care for their offspring (Komers 1996, Kishimoto & Kawamichi 1996, FitzGibbon 1997). Among monogamous birds at least, variation also exists in duration of the pair bond (Black 1996), and the extent to which socially monogamous individuals mate exclusively with their social partners (Birkhead & Moller 1992). It is almost certainly too simplistic, therefore, to consider social monogamy to be a single phenomenon that has always resulted from the same selective forces (Gowaty 1996).

1.1.4 Social monogamy and sexual fideltity

It was originally assumed that social monogamy implied mating exclusivity, but molecular techniques have revealed that this is very often not the case. Accumulating genetic data suggest that, among socially monogamous bird species, strict fidelity is the exception rather than the rule (Birkhead & Moller 1992, Hughes 1998). It was also originally thought that any extra-pair copulations (or EPCs) that did occur in socially monogamous species reflected male self-interest. It turns out that this is again often not the case. It is now widely accepted that females as well as males can gain from mating outside the pair bond (Jennions & Petrie 2000), and that socially monogamous females often actively seek extra-pair mates (e.g. Double & Cockburn 2000).

In comparison with birds, relatively few data are available on the mating behaviour of monogamous mammals (Brotherton *et al.* 1997). It remains to be seen whether, and why, they exhibit the range of genetic mating systems displayed by socially monogamous birds.

1.1.5 Monogamy in the canids

The pervasive canid social unit is the monogamous pair, although there are variations on this theme that correlate with body size (Kleiman 1967, 1967, Moehlman 1986, 1989). In the majority of larger canid species (e.g. African wild dog & grey wolf) a dominant pair is assisted by a 'pack' of subordinate 'helpers', most of which are males related to (at

least one member of) the dominant pair. Medium sized species (coyotes and jackal species) appear to be strictly socially monogamous, but may be assisted by a small number of non-breeding helpers (of either sex). In smaller species (foxes) social monogamy usually prevails, with pairs sometimes being assisted by (mostly female) helpers, and a fraction of the population occasionally breeding in polygynous groups (Moehlman 1986, Geffen *et al.* 1996).

In the vast majority of canid species males play some role in the rearing of young (Kleiman 1977, Moehlman 1979, Macdonald 1979). In most species the main parental role of males is to bring food to the lactating mother and pups (Macdonald 1992), but paternal duties also extend to guarding, huddling and transferring pups between dens (Asa & Valdespino 1998). The association between the canid pair bond with highly developed forms of paternal care has also led some authors to conclude that the need for male care was/is a critical factor favouring the origin and maintenance of monogamy in canids (e.g. Kleiman 1967, Moehlman 1986, see also Gubernick 1998, Runcie 2000). For example Moehlman (1986) states that 'among canids the pervasive theme of obligate monogamy appears to be closely linked to a critical need for paternal investment in the rearing and survival of offspring'.

A problem with theories relating the initial evolution of monogamy to the requirement for male care is that paternal care is likely to have evolved when polygyny was prevented by other factors (Clutton-Brock & Harvey 1978). In other words, it could be the association between fathers and offspring that promoted the evolution of paternal care, rather than the

other way around (Dunbar 1995). Additionally, while canid males are often heavily involved in the care of offspring, because there are no data available to assess whether, and to what degree, paternal care enhances offspring survival, it is difficult to gauge the role that male care plays in favouring the maintenance of monogamy. The observation that social monogamy persists in the absence of well-developed forms of paternal care suggests that, in some canid species at least, monogamy may be favoured largely by other factors (e.g. in Blanford's fox- Geffen & Macdonald 1992).

Very little information is available on the mating behaviour of monogamous canids. Although males' involvement in caring for offspring may imply a high levels of paternity assurance (Trivers 1972), behavioural evidence from a number of species shows that males often wander widely during the mating season, perhaps in pursuit of extra-pair mating opportunities (e.g. red fox- Voigt & Macdonald 1984). This has led Macdonald (1992) to predict that 'cuckoldry may be commonplace amongst apparently monogamous male canids once they have mated successfully at home'. At this time, only limited behavioural and genetic data are available to test this prediction.

1.2 Study species

1.2.1 The bat-eared fox

The bat-eared fox is the only canid species within the genus *Otocyon* (Kingdon 1977, Smithers 1983. They are small (average weight: 3.5kg) greyish brown animals, whose

most outstanding feature is their disproportional large ears. Bat-eared foxes are believed to be the link between the fossil genus *Protocyon* and the present day Caninae (Maas 1993), and are probably somewhat similar to ancestral canids (Asa & Valdespino 1998).

Bat-eared foxes are found in two seperate populations in Eastern and Southern Africa. It is thought that these populations were last connected during the Pleistocene (Smithers 1983). The geographic range of the southern sub species (*Otocyon megalotis megalotis)* stretches from southern Zambia and Angola to South Africa (Smithers 1983). The northern (*Otocyon megalotis vergatus*) sub species is found from Ethiopia and southern Sudan south to Tanzania (Kingdon 1977).

Unlike most other canids, the bat-eared fox has virtually given up feeding on vertebrate prey, and has become an insect specialist. Termites, and in particular a large harvester termite, *Hodotermes mossambicus*, are the preferred source of food throughout most of their range (Nel 1978, 1990, Macdonald & Nel 1986, Smithers 1983, Maas 1993). The species' reliance on harvester termites is illustrated by the fact that in southern Africa, where termite activity is subject to marked seasonal variation (being nocturnal during warmer months and diurnal during winter) foxes alter their behaviour to forage at times of maximum termite availability. Maas (1993) has also shown that in the Serengeti, bat-eared fox reproductive success is positively correlated to the density of harvester termites on their territories.

Having said this, where harvester termites are not available, bat-eared foxes have been reported to feed on other termite species (e.g. in parts of the Masai Mara bat-eared foxes feed predominantly on *Odontotermes* sp.- Malcolm 1986). They also take a variety of other insect prey. In particular, during the rainy season when termite activity can be low (Nel 1978, Waser 1980), dung beetles (*Scaraebidae*) feature strongly in the foxes diet (Maas 1993).

Rainfall may be the most important aspect of the climate for the bat-eared fox, because rainfall and insect availability are strongly correlated (Waser 1980, Nel 1978). In the Serengeti ecosystem bat-eared foxes give birth shortly after the onset of the rainy season, coinciding with the period of maximum dung beetle availability (Maas 1993), and bat-eared foxes are reported to be seasonal breeders throughout their range (Malcolm 1986, Nel 1978).

1.2.2 Bat-eared fox social behaviour

Bat-eared foxes have a flexible social system. They usually breed in monogamous pairs (Lamprecht 1979, Malcolm 1986, Pauw 2000), but also breed in small cooperative groups, which form when mature daughters delay dispersal and stay with their parents (Maas 1993). Within cooperative groups both mother and daughter usually breed (Maas 1993), with females giving birth to litters in a communal den, and suckling one another's' pups indiscriminately (Maas 1993).

Bat-eared fox males are heavily involved in direct care of young. Up to the age that pups are weaned (at approximately 14 weeks) males spend up to 90 % of their time in their close proximity, guarding, grooming and playing with cubs, while females spend the majority of their time away from the den foraging (Maas 1993). The special role of males has been attributed to the species' insectivorous diet (Lamprecht 1979, Malcolm 1986, Maas 1993); Because bat-eared foxes rely on small insects, which cannot be readily transported to the den, males are less capable of directly provisioning lactating females and pups.

Maas (1993) and Moehlman (1986) disagree about the degree to which male parental care is likely to influence offspring survival in bat-eared foxes. Moehlman argues that because bat-eared fox females seem to invest a huge amount of energy in reproduction, and because males are incapable of provisioning females and cubs, male care is unlikely to be required for successful reproduction. Maas (1993), on the other hand, argues that a lactating females commitment to prolonged periods of foraging could make male involvement in the direct care of offspring all the more important.

1.3 Principal aims of project

This research project has two primary aims: -

The first of these is to identify the factors that favour the maintenance of a socially monogamous mating system in the bat-eared fox. In particular I hope to establish the

degree to which male care is required for successful reproduction, and how this is likely to affect the optimal mating strategies of males and females. I also aim to establish the degree to which other factors, including females' spatial distribution, breeding synchrony and behaviour constrain male mating options. In doing this, I hope to shed light on both the factors that are likely to favour the maintenance of monogamy in other species of canid, and the factors that originally promoted the evolution of the canid pair bond.

The second major aim of the project is to establish whether and why bat-eared foxes mate exclusively with their social partners (i.e. if they are genetically as well as socially monogamous). In particular I seek to determine the factors that determine whether individuals seek to mate outside the pair bond, the strategies that males and females adopt to promote or constrain this behaviour, and (through genetic analysis) the proportion of fox cubs sired by males other than their social fathers.

Chapter 2

Study site & general methods

2.1 Study site

The study site was carried out on Loisaba, a private ranch on the Laikipia Plateau in central Kenya. The ranch is situated between 36° 50′ and 36° 58′ east and between 0° 63′ and 0° 74′ north, at an altitude of between 1700 and 1800 metres.

The habitat is principally open grassland (*Pennisetum straminium & Pennisetum mizianum*) with scattered shrubs (*Lycium europeum, Euclea divinorum, Rhuse natelensis, Croton sp., Grewia bicolor, Habiscus sp.*) and light acacia bush (*Acacia mellifera, Acacia drepanalobium, Acacia tortilis*) (see Figure 2.1).

The study site is home to the majority of other carnivore species found in the region. Potential fox predators regularly seen include lion, leopard, cheetah, spotted and striped hyaena, and caracal. Other resident carnivores include the serval, aardwolf, black-backed jackal and white-tailed mongoose. Common ungulates include the plains zebra, Grevy's zebra, giraffe, Grant's gazelle, oryx, eland, Coke's hartebeest and steenbok. Additional resident animal species include the aardvark and elephant.

Figure 2.1. A typical scene on the study site. This photograph illustrates the open grassland habitat, a termite mound of a *Macrotermes* spp. (the bat-eared foxes principal food) and a potential fox predator, the cheetah.

Figure 2.2 My field assistant, Evans Lemusana, handling a pair of anaesthetised adult foxes.

Mean annual rainfall on the study site between 1985 and 2001 was 493 (+/- 181) mm, making the area semi-arid (Appendix 2.1). November is the month of peak rainfall, but the majority of rain usually falls between March and July (Appendix 2.1).

2.2 Capture and handling of foxes

2.2.1 Capture of adult foxes

The majority of foxes were captured using padded foothold traps (size 2, Soft Catch®, Woodstream Corporation, Lititz, Pennsylvania 17535, USA). These traps are double staked into the ground, and buried just below the soil surface. When a fox stands on the trigger (or 'pan'), two rubberized jaws are released which clamp the animal's leg. Traps are attached to springs, which buffer the force of animals pulling against them.

I set 10-14 foothold traps in areas where I knew foxes were active (based on sightings, tracks and scats). A variety of olfactory lures (fox faeces collected from different territories, and coyote trapping lures) were used to attract foxes to traps. Traps were set in the late afternoon, and then checked at 3 hourly intervals throughout the night (9pm, midnight, 3am, 6am). Foothold traps were most often set on trails which foxes were known to use. A total of 74 foxes (13 recaptures) were caught this way.

3 adult foxes (1 recapture) were captured at den entrances using a large fish landing net. This was done by sneaking up on known den sites during the day and quickly covering

one den entrance. When foxes detected our presence they would sometimes bolt from the den and run into the net. Although this technique was undoubtedly stressful for the foxes, it had the advantage that individuals captured were never left in traps (this technique was also used to catch foxes in the Masai Mara by James Malcolm- personal communication).

2.2.2 Handling of adult foxes.

Adult foxes were immobilised using a combination of ketamine (0.5 mg/ kilo) and Medetomidine ("domitor" Orion pharmaceuticals) (0.3mg/ kilo), hand injected into the femoral muscle. The weight of trapped animals was estimated to the nearest ½ kilo prior to injection. Animals were covered with a blanket until they had gone to sleep.

I fitted at least one adult from each pair with a collar-mounted 150 Mhz radio-transmitter (Biotrack, Wareham, U.K.). Radio-collars weighed approximately 140g, which was 3.9 % of an average adults body weight (3.63 kg). Foxes were given a unique combination of coloured ear-tags (Rototags, Dalton Supplies Ltd, Henley-on-Thames, U.K.) to aid field identification. The small piece of skin made by the ear punch was collected (for genetic analysis), and stored in TES buffer (100mM Tris HCl, 100mM EDTA, 2 % sodium dodecyl sulphate).

Foxes were then sexed, weighed and measured. Body measurements taken were head-body length, head width, hindfoot length (left and right) and ear length (left and right). Additionally individuals were scored (on a nominal scale) for incisor wear (an estimation

of age, after Harris 1988) and the prevalence of ectoparasites (ticks and fleas). The reproductive state of females (whether they are in oestrus, pregnant or lactating) was noted, as was male testis size (length and width).

Before release, foxes were injected with atipamezole ("antisedan" Orion pharmaceuticals), to reverse the effect of the metatomidine. Foxes were then held in a wooden box for 1 hour, until the effects of ketamine had worn off, before being released at the capture site.

2.2.3 Capture and handling of cubs

Fox cubs were captured in 2 ways: -

When cubs were small (less than about 4 weeks) it was often possible to reach inside dens and capture them by hand. If cubs were in deeper or less accessible dens, I first attracted them to den entrances by playing an audio recording of a suckling bat-eared fox litter, which often attracted cubs to the den entrance (obtained from the BBC Natural History Unit, Bristol, U.K.). This technique was only used when adults were known to be away from the den, and never led to litter abandonment. 28 cubs (from 9 litters) were captured this way.

As cubs got older, they became more difficult to capture by hand. Cubs that were not caught during the first 4 weeks of their life were later captured using foothold traps after

they reached 14 weeks of age (and were approximately half grown). 15 cubs were captured this way (between the ages of 14 and 24 weeks).

I handled all cubs (both those below the age of 4 weeks and above the age of 14 weeks) without using anaesthetic. Cubs were sexed and weighed, and a small tissue sample (from the tip of the tail) was taken for DNA analysis. Cubs over 14 weeks were also fitted with coloured ear-tags.

Small cubs, and cubs captured near dens, were released into their dens. Larger cubs captured away from dens were released at the trapping site.

2.2.4 Ethical note on capture and handling techniques

All techniques used in the project were approved by the Kenya Wildlife Service (research permit number MOES&T 13/001/C 689).

During the course of the study no foxes were seriously injured or killed during capture, either by traps or by larger carnivores. The most serious injuries incurred in foothold traps were breaks in the skin on the capture foot (n=2), and no individuals showed noticeable long-term effects of these injuries.

Although bat-eared foxes did not usually struggle when they were captured in foothold traps (and hence did not draw attention to themselves) it is likely that if larger carnivores

found them they would make easy prey. I consider it to be somewhat fortuitous that this no foxes were killed in this manner, and stress that future researchers using this capture technique need to be aware of this risk.

2.3 Radio-tracking techniques

2.3.1 General radio-tracking techniques

Radio-tracking was carried out in a car (at night) and on foot (during the day), using a receiver (Telonics, Mesa, Arizona, USA) and a 3-element yagi antenna. Radio-collars were generally detectable from distances of up to 1.0 km, and had a 12-15 month field life.

Obtaining locations by triangulation

Nocturnal locations of foxes were estimated by triangulation. This technique works by taking transmitter bearings (based on the direction of the strongest radio-signal) from two locations, and working out the point of bearing intersection (an estimate of an animals location). Locations were recorded using a handheld GPS (Garmin II, Garmin, USA).

The time taken between fixes was kept as short as possible, in order to minimise error resulting from animal movement (Kenward 1987). Fixes taken more than 10 minutes apart being discarded, and the average time between fixes (based on 500 triangulations from the data set) was 6.30 +/- 2.00 minutes. I always attempted to obtain angles of 90

degrees between the 2 fixes in order to maximise triangulation accuracy (Kenward 1987), and angles of less than 40 degrees (or more than 140 degrees) were discarded. The average deviation from a 90 degree angle (based on 500 fixes from the data set) was 21.4 +/- 13.9 degrees.

Time taken between successive fixes on the same animal

In order to maximise information content of each radio-tracking location (by reducing the spatial autocorrelation of data, see Swihard & Slade 1985), I allowed a minimum interval of 3 hours between successive triangulations on the same animal. This follows the rule of thumb that, in order to achieve spatial independence of locations, the minimum time taken between fixes should be greater than the time it takes an animal to cross it's territory (Swihard & Slade 1985). Behavioural data (presented in chapter 4) showed that foxes regularly crossed their entire territories in this space of time.

Accuracy of triangulations

Radio-telemetry accuracy can be affected by mapping error, signal bounce, vegetation cover, electromagnetic interference, animal movements, operator error and distance to radio-tagged animals (White & Garrot 1990, p28). Despite the importance of establishing whether data are accurate enough to meet study objectives (see chapter 5 for example), few studies using telemetry (to obtain locations) provide adequate measures of triangulation error (see Withey *et al.* 2001 for review).

I estimated triangulation error by estimating daytime locations of foxes by triangulation, walking in on animals to establish their actual locations, and calculating linear error (a beacon test-White & Garrot 1990, Withey *et al.* 2001). Although this method of estimating error has a number of flaws (animals were not moving, as they do at night, and test conditions may have reduced operator error) it provided an estimate of minimum error.

I found that the average error of 50 test fixes was 141 +/- 111m. Although animal movement could have further reduced the accuracy of nocturnal triangulations, the angle between fixes used to calculate nocturnal locations was closer to 90 degrees (average deviation 21.4 degrees) than those used in this beacon test (average deviation 24.4 degrees), and data from the beacon test showed that location error was positively correlated with increasing deviation from a 90 degree angle (Pearson test, $r=0.44$, $d.f.=48$, $p<0.01$).

Spatial error can also arise in radio-tracking studies if the observation rate (the probability of successfully obtaining a location when a triangulation is attempted) is low, and animals are consistently not located in certain areas on or off territory (Garton *et al.* 2001). In a sample of data collected between March and June 2001, individuals were successfully located on 290 of 300 (or 96.7% of) attempts. This shows that (low) observation rate is unlikely to have significantly affected the accuracy of data presented in the thesis.

2.3.2 Interaction of foxes in space and time

The relationship between the movement patterns of two animals in space and time (or 'dynamic interaction'- Doncaster 1990) can be investigated by collecting 'simultaneous' locations from the animals, and comparing observed separation distances with those expected by chance (based on a random recombination of all observed locations).

I obtained 'simultaneous' locations from dyads of foxes by moving through the study site triangulating duos of animals (mated partners and neighbours) as close together in time as was logistically possible. Whenever possible I triangulated animals from the same locations. This was usually possible for paired animals, which spend the majority of their time in close proximity, but was less often possible for neighbouring foxes. Fixes obtained within 20 minutes of each other were considered to be 'simultaneous', as a cut-off time less than this would have made it difficult to collect sufficient data from neighbouring foxes.

Dynamic interaction analyses were carried out using the Wildtrak computer program (Todd 1992). The observed and expected frequencies at which animals were found within certain distances of each other were compared using X^2 tests (with 1 d.f.).

2.3.3 Calculation of home range size and overlap

Choice of home range estimators

Home range size (and overlap) was calculated using both Minimum Convex Polygons (here-after MCP) and Kernel range estimators. Both techniques have advantages and disadvantages that make them more or less appropriate for different types of analysis (see Kernohan *et al.* 2001 for review): -

MCP ranges are constructed by drawing a line around the outermost locations recorded for an animal (Kenward 1987). They thus estimate the minimum area within which all fixes are located. One problem often attributed to MCP's is their over-sensitivity to outlying data points (Kernohan *et al.* 2001). Because of this, a standard adjustment is to remove 5% of outlying fixes (White & Garrot 1990). For certain types of analysis, however, sensitivity to outlying data points may be advantageous. If, for example, one is particularly interested in excursions outside of the normal foraging range, the MCP technique (including outlying data points) may be most appropriate.

Unlike the MCP technique, which only considers distances between data points, Kernel home range calculating techniques work by describing the relative frequency distribution (density) of locations (Worton 1989). The Kernel technique is better able to cope with irregularities in non-uniformly shaped home ranges (e.g. ranges with multiple centres of activity), is less sensitive to outlying data points, and requires fewer fixes for an accurate

estimate of home range size (Kernohan *et al.* 2001). Because of this, the Kernel technique is thought to provide a more accurate estimate of an animal's regular foraging range.

Analyses of MCP and Kernel home range sizes and overlap were carried out using the animal movement extension of Microsoft compatible programme Arcview (Hooge & Eichenlaub 1997). Kernel ranges were estimated using the Least Cross Squares Validation (LCSV) smoothing parameter, as currently recommended in the ecological literature (Seaman *et al.* 1999).

Removal of outlying data points

Because some analyses I performed were particularly concerned with outlying data, and those that weren't were conducted using Kernel ranges (which are relatively insensitive to outlying data) I attempted to remove only those outliers that clearly resulted from radio-tracking error. In order to achieve this, while radio tracking, I always noted when animals appeared to be outside their usual foraging range. Outlying data points were only removed if the animal's location had not been noted as being unusual and/or if outlying data were clearly beyond the radio-collar's signal range.

Number of fixes required to assess home range size

The sample size of radio-fixes required to give a valid measure of home range size depends on the movement patterns of the animal, the radio-tracking protocol, and the

method of home range analysis used (White & Garrot 1990, Kernohan *et al.* 2001). Several authors have used field data and computer simulations to determine sample size requirements, and results are often contradictory. For example, Gese *et al.* (1990) found that the minimum sample size required to construct coyote home ranges varied from 23-36 (using the area observation curve), while several studies report that sample sizes of over 100 fixes are required for an accurate estimate of MCP ranges (e.g. Bekoff & Mech 1984, Harris *et al.*1990). After reviewing literature on the subject, Kernohan *et al.* (2001) recommend using a minimum of 50 independent locations. In this study, I calculated home range sizes based on 60 locations. Two lines of evidence suggested that this sample size provided an adequate estimate home range size: -

Firstly, Minimum Convex Polygon (MCP) sample size bootstraps, conducted to investigate the effect of the number of radio-tracking fixes on MCP area, showed that although MCP range sizes had not necessarily reached an asymtote after 60 fixes, they appeared to stabilize after approximately 50 fixes (see Appendix 2.2).

Secondly, MCP ranges based on 30 fixes were on average 72.2 % (+/- 8.52, n=20) of the size of those based on 60 fixes, while Kernel ranges based on 30 fixes were on average 89.1% (+/- 5.93, n=20) of the size of those based on 60 fixes. This further demonstrates that, using the radio-tracking protocol adopted in this study, bat-eared fox home range sizes stabilize after relatively few fixes, particularly when using the Kernel technique.

2.4 Habituation and behavioural observation

2.4.1 Habituation and observation technique

Foxes were habituated to the presence of a vehicle by slowly following active foxes to within approximately 50m (driving a Toyota Landcruiser in 1st or 2nd gear). Some fox pairs required little or no habituation, while others had to be followed (for 3 hour periods) up to six times before they appeared comfortable in the vehicles presence (i.e. they would walk slowly, feed and sometimes approach the vehicle).

Foxes were observed from a vehicle, using a spotlight and a pair of 8x40 binoculars. Observations were typically made between 10 and 40 metres of foxes, although some individuals would occasionally approach to within a few metres of the vehicle. With good moonlight, it was sometimes possible to observe foxes without the use of the spotlight. When the spotlight was used, effort was made to observe foxes in the periphery of its beam, and only for short periods of time.

Observation sessions lasted 3 ½ hours, during which the behaviour and location of foxes was recorded instantaneously (after Altmann 1974) at ten minute intervals. In addition to recording behaviour (see below), when two or more foxes were present, I recorded the distance between them, and which animal was responsible for maintaining proximity (the first animal to clearly move towards the other).

2.4.2 Categorization of behaviour

Fox behaviour was classified behaviour into one of the following 5 categories: -

i) walk- walking with head held up.

ii) search walk- walking slowly with held horizontally or towards ground, typical of foraging foxes.

iii) feed- standing still or moving very slowly with head held to the ground, suggesting that animals are consuming food.

iv) rest- recorded when animals were either sitting, lying or inside dens.

v) other- recorded when foxes were engaged in activities that didn't fall into the categories defined above, such as standing, running or playing.

2.5 Observation schedules

In order to control for the fact that ranging patterns, interaction rates and behaviour of foxes might vary according to the time of night, I split the night into arbitrary 3 time blocks; 6.30-10.30 pm, 10.30-2.30 am & 2.30-6.30 am, and collected approximately equal amounts of behavioural and radio-tracking data from each time block (see method sections in chapters 3, 4 & 5 for more details).

2.6 Measurement of territory quality

I assessed territory quality and vegetation type on territories by measuring termite abundance and vegetation characteristics in twenty-five randomly placed $1m^2$ plots on each territory. Random locations were calculated within MCP home ranges using the *generate random points* function of Arcview (animal movement extension, Hooge & Eichenlaub 1997), and located using a hand-held GPS. Within each $1m^2$ plot I measured:-

1) Number of termite foraging holes (after Maas 1993).
2) Predominant vegetation type (grass, herb, shrub or tree).
3) Proportion of ground covered by vegetation height.
4) Maximum vegetation height.

Territory quality was expressed in terms of: -

1) Termite densities (the average number of foraging holes per square metre -after Maas 1993).
2) Territory size (since termite densities were not found to be related to territory size).
3) Total termite abundance (=territory size x termite abundance).

Chapter 3

The effects paternal care and territory quality on reproductive success; implications for the maintenance of social monogamy

3.1 Introduction

3.1.1 Paternal care in mammals

Male care has been defined by Woodroffe & Vincent (1994) as 'any post-fertilization behaviour that benefits the young and that the male would not carry out if the young were not present'. Although this definition refers to care provided by all males (and not just fathers), it applies equally well as a description of paternal care. Their term does not necessarily imply energetic or reproductive costs to the caregiver, as do the expressions 'parental expenditure' and 'parental investment' (Clutton-Brock 1991).

Theoretical research into the evolution of paternal care has focussed on examining the trade-off between the relative costs and benefits of providing care for offspring (Dawkins & Carlisle1976, Maynard Smith 1977, 1982, Clutton-Brock 1991). The principle benefit of male care is that it may facilitate offspring growth and survival (Clutton-Brock & Godfray 1991), while the principle cost is assumed to be a reduced opportunity to mate with additional females (Trivers 1972). Clutton-Brock (1991, p.106) summarized the

situation, stating that 'selection should favour desertion by one parent when the chance of breeding again is high, the current brood requires little extra attention, and the parent's contribution to parental care is small'.

In light of this it is somewhat surprising that any male mammals care for their offspring; female mammals commitment to lengthy period of gestation and lactation means that not only is there limited scope for males to assist in offspring care (Orians 1969), but males also have every opportunity to desert females and seek additional mates (Trivers 1972). Nonetheless, in between 5 and 10 % of mammal species males provide some form of care for their offspring (Kleiman 1977, Kleiman & Malcolm 1981, Woodroffe & Vincent 1994). Paternal care occurs most often in the rodents (Elwood 1983), carnivores (Kleiman & Malcolm 1981) and primates (Dunbar 1988), and is most regularly found in species living in small, closely related social groups, where monogamous mating is the rule (Kleiman & Malcolm 1981).

Woodroffe & Vincent (1994) provide a thorough review of the forms of male (not necessarily paternal) care observed across mammals. They point out that, other than lactation, fathers from a range of species exhibit all of the parental behaviours shown by mothers. Forms of parental care can be divided into those where the benefits (per offspring) decline as brood size increases ('depreciable') and those where benefits do not decline with brood size ('non-depreciable', after Altmann *et al.* 1977). Examples of depreciable forms of care are grooming, carrying and in particularly feeding young. Non-

depreciable forms of care could be huddling with young or remaining vigilant for predators.

3.1.2 Paternal care in the canids

In the majority of canid species fathers, and sometimes non-breeding helpers, provide some care for offspring (reviewed in Kleiman & Eisenberg 1973, Moehlman 1986,1989, Asa & Valdespino 1998). An important element of this care is often the provisioning of the female and her litter. This allows females to spend more time at dens directly caring for cubs, and perhaps to invest more heavily in reproduction (Kleiman & Eisenberg 1973). In the medium and larger sized canids, males often regurgitate food (African wild dog- Malcolm & Marten 1982, Grey wolf- Mech 1970), whereas in the smaller canids, food items are usually carried back to the den (Arctic fox- Stand *et al.* 2000, Red fox- Macdonald 1979).

Field studies of bat-eared foxes have revealed that, in this species, with the exception of lactation, the parental roles of males and females are reversed (Lamprecht 1979, Malcolm 1986, Maas 1993, Pauw 2000). Males spend significant amounts of time at breeding dens, and are involved in many aspects of direct cub care, while females spend the majority of their time foraging away from dens. The special role of males is probably attributable to the fact that small food items (in their case termites) are not readily transported back to the den in any form other than milk (Maas 1993). The racoon dog,

which also feeds on small food items, shows a similar pattern of paternal and maternal care (Kauhala *et al.* 1998).

3.1.3 Paternal care and the evolution and maintenance of monogamy

The adaptive nature of paternal care is central to many theories concerned with the origins and maintenance of monogamy (Orians 1969, Trivers 1972, Emlen & Oring 1977, Wittenberger & Tilson 1980, Clutton-Brock 1989, 1991).

It has been proposed that the requirement for male care may have promoted the evolution of monogamy (Kleiman 1977, Moehlman 1986). This is difficult to ascertain, however, because the factors that originally promoted the evolution of a particular mating system may differ from those favouring its current maintenance (Clutton-Brock & Harvey 1978; this is discussed further in chapters 4 & 6).

The role paternal care plays in the maintenance of monogamy is easier to establish, because it requires identification of the current requirement for male care: -

It is possible that the expression and requirement of male care have evolved to the point that male care is essential for any degree of reproductive success (Kleiman 1977, Wittenberger & Tilson 1980, Gowaty 1996). Under these circumstances males are forced to stay with mates and help rear offspring, and social monogamy is obligatory. Similarly the requirement of male care may have evolved to the point that males dividing their care

between multiple litters suffer reduced reproductive success (so males are less successful with 2 mates than 1- after Wittenberger & Tilson 1980, although their hypothesis also considers how polygyny affects resource access and predation risk). Under these circumstances social monogamy would again be the preferred mating system of both sexes.

Alternatively, the benefits of paternal care may be such that males do better breeding in polygynous groups, but females always do better breeding in monogamous pairs. When this occurs a conflict of interest exists between males and females, and each sex is expected to adopt strategies that promote their interests over those of the opposite sex (e.g. Davies 1992, Ahnesjo *et al.* 1993). If social monogamy persists under these circumstances, males can be described as being 'failed polygynists' (Birkhead & Moller 1996). Studies on a number of avian species confirm that while males benefit through polygyny, females often suffer the cost of reduced paternal investment (Davies 1992, Slagsvold & Lifjeld 1994, see Bensch 1997 for other costs associated with polygyny).

If polygyny is never the best option for unmated females, they should try to avoid being recruited onto the territories of males who already have partners (Lundberg & Alatalo 1992). Similarly, if polygyny decreases the reproductive success of paired females, they are expected to aggressively exclude additional females from their territories (the female-female aggression hypothesis- Wittenberger & Tilson 1980, Gowaty & Wagner 1988, Gowaty 1996). Studies of monogamous species from several taxa suggest that female-female aggression plays an important role in maintaining social monogamy (mammals;

Brotherton & Manser 1997; birds- Sandell 1998, Slagsvold *et al.* 1999; fish- Kokita 2002).

3.1.4 The relationship between paternal care and paternity

Trivers (1972) was the first to suggest that males should be under strong selective pressure not to invest in offspring that they have not fathered. He predicted that it would be adaptive for males to adjust levels of paternal investment according to their confidence of paternity.

Subsequent models of the relationship between paternity and paternal care have shown that such a facultative adjustment of male care is expected, but only under certain conditions (reviewed in Wright 1998 & Sheldon 2002). If males are unable to accurately assess their paternity, if adjustment in care has no affect on future reproductive success, or if males cannot expect higher levels of paternity in future breeding events, then no alteration of paternal behaviour is expected (Maynard-Smith 1977, Grafen 1980, Westneat & Sherman 1993). Empirical studies confirm that in some species males do adjust levels of investment according to their confidence of paternity (e.g. Dixon *et al.* 1994, Sheldon & Ellegren 1998, reviewed in Sheldon 2002).

It follows that the costs to females of engaging in extra-pair copulations are potentially greatest in species where male care has a large effect on offspring survival (Gowaty 1996, Birkhead & Moller 1996, Stanback *et al.* 2002). Related to this prediction, Moller

(2000) and Moller & Cuervo (2000) have demonstrated that across monogamous bird species, levels of extra-pair paternity (the proportion of young sired by males other than their social fathers) are generally higher in species where males play a relatively small role in the successful rearing of offspring (although the cause of this cross-species association has been debated; c.p. Wright 1998, Moller 2000, Sheldon 2002).

3.1.5 The adaptive significance of paternal care in mammals

In order to understand the role that paternal care plays in maintaining monogamy (section 3.1.2) and mediating the costs and benefits of mating outside the pair bond (section 3.1.3), it is necessary to know if and to what extent paternal care enhances offspring survival. While substantial data are available on this subject for birds (see Bart & Tornes 1989, Gowaty 1996 for reviews), almost nothing is known about the adaptive nature of male care in mammals.

Because of the difficulties associated with collecting detailed field data, the majority of mammalian studies are restricted to observing patterns of care and making educated guesses about its likely effect on offspring survival (Clutton-Brock 1991). The few detailed data that are available mostly come from captive studies of monogamous rodents.

Wynne-Edwards and Lisk (1989) have demonstrated that the presence of a father increases offspring survival in captive Djungarian hamsters. Similarly it has been

demonstrated that male presence increases offspring survival in captive California mice, but only if temperatures are low, or if females are forced to forage on a running wheel to obtain food (Brown 1993, Cantoni & Brown 1997). Only one study has convincingly demonstrated that male care increases offspring survival under natural conditions; Gubernick & Teferi (2000) used male removal experiments to demonstrate that male presence increases pup survival in a wild population of California mice.

3.1.6 Factors affecting reproductive success in canids.

The fact that canid fathers are often closely involved in offspring care (section 3.1.2) suggests that their help is likely to increase offspring survival, particularly in species where males directly provision females and cubs. In addition, the observation that canids have large litter sizes and long periods of dependency (relative to other mammals) suggests that investment of more than one parent may often be required for successful reproduction (Kleiman & Eisenberg 1973).

However, while there are some data relating canid reproductive success to food availability (e.g. Angerbjorn *et al.* 1991; Englund 1970, Maas 1993), no studies have demonstrated that paternal care enhances offspring survival. Having said this, there is indirect evidence suggesting that this is most likely the case. For example, the observation that the presence of non-breeding helpers (which provide the same forms of care as males) increases reproductive success in black-backed jackals (Moehlman 1979, 1986), red foxes (Macdonald 1979) and African wild dogs (Creel & Creel 2002) implies

that male care is also likely to increase offspring survival (though these studies did not control for the confounding effects of territory quality).

Moehlman (1989) and Maas (1993) have both suggested that female bat-eared foxes invest very heavily in reproduction, even relative to other canids (see Maas p. 55). Combining this with the observation of a widowed female successfully rearing a litter of 5 cubs (made by Maas), Moehlman (1989) concluded that female bat-eared foxes are capable of providing the majority of the required parental investment. Maas, however, suggests that the success of this widowed female probably resulted from exceptionally high food availability, and that under normal circumstances females would be unable to provide direct care for cubs and spend a sufficient amount of time foraging.

Clearly, data are required to establish the degree to which paternal care affects offspring survival in bat-eared foxes, and other canid species.

3.1.7 Aims of chapter

This chapter investigates the parental roles of bat-eared foxes on the study site, and the relative degree to which paternal care and territory quality affect reproductive success. In doing so, I hoped to shed light on the role (if any) paternal plays in maintaining monogamy, and mediating the costs and benefits of engaging in extra-pair copulations. I did this by establishing: -

1) Extent and variation in den attendance within and between the sexes.

I examined inter and intra-sexual differences in parental behaviour by establishing the proportion of time individual males and females spent at or near breeding dens. These data were also analysed to see how the parental behaviour of mated pairs was co-ordinated, and how patterns of den attendance varied with cub age.

2) Forms of care provided by males and females, and reproductive tactics of a widowed female.

In order to further shed light on the parental roles of males and females, I established the forms of care they provided for cubs through the direct observation of adults at breeding dens. Immediately prior to the onset of collecting these data, an adult male from one pair was killed (by a large carnivore species). This allowed me assessment of the parental tactics and breeding success of a widowed female.

3) The energetics of female reproduction.

I compared time budgets of lactating females with those of gestating and non-breeding females in order to establish the extent to which females are capable of increasing food intake during lactation, and to estimate how much 'free time' they have available to expend on direct cub care. During the course of the project, I observed that all female mortality occurred during lactation. I calculate whether female mortality occurred significantly more often during lactation, and whether or not it was associated with low food availability.

4) If and to what extent male care and territory quality affect reproductive success.

I investigated the adaptive significance of male care by calculating if and to what extent measures of male den attendance and territory quality were associated with reproductive success.

3.2 Methods

3.2.1 Den attendance of breeding adults

During the 2001 breeding season, nocturnal locations of male and female foxes with pre-weaned cubs were calculated using radio-telemetry (section 2.2), and straight-line distances to active den site were calculated. Data were collected from birth up until cubs were weaned (at 14 weeks- Maas 1993), and divided into 7 bi-weekly cub age classes (0-2, 2-4, 4-6, 6-8, 8-10, 10-12 & 12-14 week). When more than one fix was obtained per night (on any individual fox), a minimum time of 3 hours was allowed between fixes.

Data are presented and analysed for 6 males and 5 females for which more than 30 fixes were obtained. Data are classified according to the number of observations within 5 distance categories from the den (0-100m, 1-200m, 2-300m, 3-400m, 400m+). For both males and females, the proportion of fixes collected during different cub age classes did not differ significantly between individuals (for males- X^2=25.6, d.f.=30, p=0.71; for females- X^2=30.4, d.f.=24, p=0.17). Because of this, when considering den attendance of individual males and females, data were combined across cub age class. For the same reason, when considering the effect of cub age on den attendance, data from different individuals were combined.

One tailed t-tests were used to compare the proportion of time males and females spent within given separation distances of dens, because we hypothesised that males would

spend more time close to and less time far from dens (see section 3.1.2). Chi-square tests were employed to investigate intra-sexual differences in the proportion of time individual males and females were found within given distance categories.

The degree to which mated partners from 4 pairs co-ordinated parental behaviour was investigated by comparing observed and expected frequencies of simultaneous presence at (within 200m of) breeding dens. Expected frequencies of simultaneous presence were calculated by multiplying the frequencies at which male and female partners were found (alone or together) within 200m of their dens. Chi-square tests (with one degree of freedom) were used to compare observed and expected frequencies.

No more than two adults were ever observed at or in vicinity of breeding dens (appendix 3.2), and all breeding animals were individually marked (with coloured ear-tags). This confirms that no additional foxes were involved in any breeding attempt. This ties in with the fact that, during the run up to the 2001 birthing season, foxes on the study site were always encountered in pairs (particularly during the day- appendix 3.1).

3.2.2 Forms of care provided by adults

During the 2002 breeding season, when foxes were deemed to be sufficiently well habituated, the parental behaviour of 4 fox groups was investigated through the direct observation of adult foxes at breeding dens. The purpose of collecting these data was to establish the forms of care that males and females provided for cubs.

Breeding dens were observed during 3 ½-hour observation periods, and data on the behaviour and proximity of adult foxes and cubs (to dens) were recorded at ten-minute intervals (giving a total of 20 observations per session). When foxes were not at or within sight of dens, proximities were estimated according to the strength of their radio-signal. Although there may have been a degree of inaccuracy in this technique, it gave an idea of whether an animal was 'in the area', and allowed a rough estimate of den proximity.

Immediately prior to the onset of data collection, the adult male from one fox pair was killed by an unidentified predator. This allowed me to assess the parental tactics and reproductive success of a widowed female. I hypothesized that if males were found to spend more time close to breeding dens than females, and that this behaviour increased cub survival, the widowed female would adjust it's behaviour and spend more time at or close to it's breeding den (than other females).

3.2.3 Time budgets and mortality of lactating females

Time budgets of 3 lactating females were obtained through behavioural observation. 3 observation sessions were carried out on each female, once during each nocturnal time block (section 2.5). During each observation session, female location and behaviour were recorded 20 times at 10-minute intervals. Behaviour was classified into one of the categories defined in section 2.3.3. Chi-square tests were used to compare time budgets

with those collected (from the same 3 females) during the pre-mating, mating and gestation periods.

During the course of the project, it became apparent that all observed female mortality occurred during the lactation period. We tested to see if females were dying significantly more often during lactation (than outside lactation) by calculating the proportion of deaths that we would have expected during and outside of lactation (given a lactation period of 14 weeks- Maas 1993), and using a chi-square test (with 1 d.f.) to compare observed and expected number of deaths. t-tests were used to compare territory quality (see 3.2.4 below) of females that died with those that survived (lactation).

3.2.4 Analysis of factors affecting reproductive success

We investigated the relationship between male den attendance, territory quality and the following 4 measures of reproductive success: -

1) Number of cubs born= maximum number of cubs first seen at first emergence, or maximum number of cubs captured from each litter.
2) Number of cubs weaned= number of cubs surviving to 14 weeks.
3) Number of cubs dispersing= number of cubs surviving to 6 months.
4) Proportion of cubs surviving= proportion of cubs in a litter surviving from birth to weaning.

Den attendance was classified as the proportion of the night that males spent within 200m of breeding dens. This measure was highly correlated with the proportion of time spent within 100m of dens ($r=0.95$, d.f.=9, $p<0.001$), and results of analyses did not differ according to which measure was used. For 8 breeding attempts den proximities were established using nocturnal radio-tracking data (section 3.2.1), using a minimum of 24 radio-tracking fixes per male per breeding event ($\bar{x}=36.9$, s.d.=8.6). For a further 3 breeding events, den proximities were established through the direct observation of breeding dens (section 3.2.2, with data coming from a minimum of six 3 ½ hour observation sessions per breeding event- see Table 3.3).

Territory quality was measured in terms of termite foraging hole density (see section 2.4), territory sizes (based on 60 radio-tracking fixes, using the MCP and Kernel techniques- section 2.2), and total termite availability on MCP and Kernel territories (termite density x territory size).

Initially, single regression analyses were performed to establish if and to what extent male den attendance and territory quality explained variation in reproductive success. Because male den attendance and measures of territory quality both explained significant variation in some measures of reproductive success, multiple regressions were performed to establish their relative effects. In these analyses male den attendance was regressed with MCP range size, because this measure (of territory quality) was the best predictor of reproductive success in the single regressions. Multiple regressions were restricted to investigating effects on the number and proportion of cubs reaching weaning, because too

few data were available to investigate effects on the number of cubs reaching dispersal (n=7).

3.3 Results

3.3.1 Nocturnal den attendance of adults with pre-weaned cubs

During the 2001 breeding season, data were collected to determine the amount of time male and female foxes spent in the vicinity of breeding dens at night. These data were collected in order to establish: -

1) the extent of and variation in den attendance between and within the sexes

2) if and how den attendances of males and/or females varied with cub age

3) if and how the behaviour of mated partners was co-ordinated

Do levels of den attendance differ within or between the sexes?

Data on the nocturnal proximities of 6 male and 5 female foxes (for which more than 30 fixes were obtained) to breeding dens are presented in Table 3.1 and Figure 3.1. As expected males spent significantly greater proportions of their time close to breeding dens than did females; on average males spent 36 % and 56 % of their time within 100m and 200m of breeding dens, whereas females spent 18.8 % and 30.8 % of their time within these separation distances (1-tailed t-tests: for 0-100 m category- $t=2.48$, d.f.=9, $p=0.02$, for 1-200m category- $t= 2.00$, d.f.=9, $p=0.05$). Also expected was the fact that females spent significantly greater proportions of time than males furthest from breeding dens (for 400m + category- $t=-2.97$, d.f.=9, $p<0.02$). There were no significant differences between males and females in the proportion of time spent in the 2-300m and 3-400m categories

Table 3.1 Nocturnal proximities of 6 male and 5 female foxes with pre-weaned cubs to breeding dens. Data are combined across cub age classes (numbers in parenthesis are the number of fixes collected for each of the 7 cub age classes). Proximities are expressed as total number (and %) of observations within given separation distances, and mean (and s.d.) % values are given for each sex.

		Total	*Distance to den*				
Animal ID	*Sex*	*no. fixes*	0-100m	1-200m	2-300m	3-400m	400m+
Fm9	M	39 (2,6,7,5,6,6,7.)	7 (17.9)	7 (17.9)	11 (28.2)	4 (10.3)	10 (25.6)
Fm17	M	46 (3,11,5,5,6,8,8.)	28 (60.9)	8 (17.4)	3 (6.5)	5 (10.9)	2 (4.3)
Fm20	M	35 (8,5,5,7,6,4,0.)	15 (42.9)	9 (25.7)	3 (8.6)	2 (5.7)	6 (17.4)
Fm25	M	40 (2,10,6,5,6,8,3.)	15 (37.5)	9 (22.5)	8 (20)	5 (12.5)	3 (7.5)
Fm27	M	44 (7,6,8,5,7,4,8.)	11 (24.4)	8 (17.8)	10 (22.2)	1 (11.4)	11 (24.4)
Fm31	M	43 (6,6,8,6,6,6,5.)	14 (32.6)	8 (18.6)	10 (23.3)	2 (4.7)	9 (20.9)
		$\bar{x}$	36.0	20.0	18.1	9.3	16.7
		s.d.	15.1	3.4	8.7	3.2	8.9
Ff28	F	38 (7,7,8,5,7,3,1.)	9 (23.7)	8 (21.1)	5 (13.2)	3 (7.9)	13 (34.2)
Ff16	F	41 (3,9,7,5,6,8,3.)	8 (19.5)	1 (2.4)	5 (12.2)	9 (22.0)	18 (43.9)
Ff29	F	41 (9,8,4,7,6,4,3.)	4 (7.3)	3 (7.3)	1 (2.4)	4 (9.8)	29 (73.2)
Ff46	F	34 (0,3,7,6,5,6,7.)	7 (20.6)	3 (8.8)	3 (8.8)	1 (2.9)	20 (58.8)
Ff47	F	39 (1,10,5,5,6,8,4.)	9 (23.1)	8 (20.5)	7 (17.9)	7 (17.9)	8 (20.5)
		$\bar{x}$	18.8	12.0	10.9	12.1	46.1
		s.d.	6.7	8.3	5.8	7.7	20.6

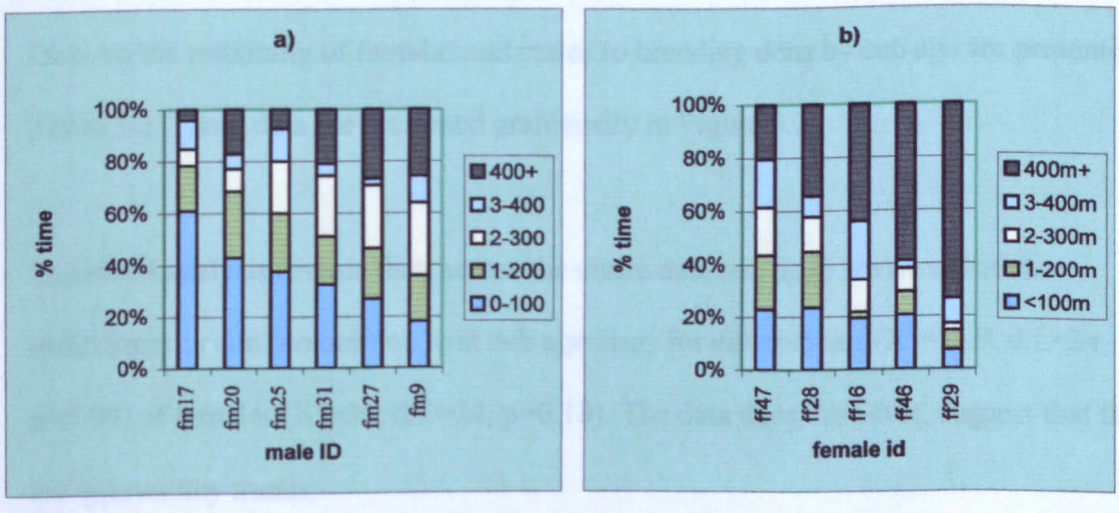

Figure 3.1 Proximities of 6 individual males a) and five individual females b) to breeding dens. Data are combined across cub age classes.

(2-300m- t=1.65, d.f.=9, p=0.06, 3-400m- t=-0.77, d.f.=9, p=0.24). The data confirm that, on average, males spend more time than females at or close to breeding dens.

The data reveal considerable inter-individual differences in den proximity, among both males (Figure 3.1a) and females (Figure 3.1b). Statistical analysis reveals that this variation is highly significant (for males- X^2=40, d.f.=20, p<0.01, for females- X^2=43.4, d.f.=16, p<0.01). Variation was such that male fm17 was found within 100m of his den three times more often, and within 200m twice as often, as males fm9 & fm27. Similarly, females ff47 and ff28 spend more than twice as much time within 100m and 200m of their dens than female ff29. Also worth noting is the fact that the den proximities of females ff28 and ff47 were similar to those of males fm9 and fm27. Interestingly fm27 and ff28 were paired animals.

Do levels of male or female den proximity vary with cub age?

Data on the proximity of females and males to breeding dens by cub age are presented in Table 3.2. These data are presented graphically in Figure 3.2.

Statistical analysis reveals that, across the entire data set, there are no significant differences in den proximities with cub age class for either males (X^2=33.9, d.f.=24, p=0.09) of females (X^2=30, d.f.=24, p=0.18). The data does, however, suggest that there are noteworthy trends: -

For males, there was little variation in den proximity with cub age, particularly when cubs were aged between 2 and 12 weeks. However, between cub ages 0-2 weeks and 12-14 weeks males spend less time close to breeding dens (but only data from the 0-2 week category differed significantly from the rest of the data set; 0-2 week- X^2=9.54, d.f.=4, p=0.05; 12-14 week- X^2=5.5, d.f.=4, p=0.25).

Females spent increasing amounts of time close to breeding dens as their cubs increase in age. Statistical analysis reveals that the correlation between cub age and % of time females were within 100 m of breeding dens approaches significance (Pearson test, r=0.65, d.f.=5, p<0.1), while the correlation between cub age and % time within 200m is significant (r=0.94, d.f.=5, p<0.01). The drop in proportion of time males and females spend within 100 m of dens when cubs reach 14 weeks of age may reflect the fact that, by this age, cubs start to forage further from their dens (see section 3.3.2).

As the den proximities of females increased with increasing cub age, so inter-sexual differences in den proximity decreased. During the first 2 weeks of cub life neither sex spent much time close to breeding dens, and male and female den proximities did not differ significantly (0-2 weeks- X^2=3.15, d.f.=4, p=0.53). Between cub ages of 2 and 6 weeks males spend significantly more time close to breeding dens than females (2-4 weeks- X^2=27.7, d.f.=4, p<0.01, 4-6 weeks- X^2=13.4, d.f=4, p<0.05). After this, although males continued to spend more time closest to breeding dens, differences were not statistically significant (6-8 weeks- X^2=4.69, d.f.=4, p=0.32, 8-10 weeks- X^2=7.89, d.f.=4, p=0.1, 10-12 weeks- X^2=7.19, d.f.=4, p=0.13, 12-14 weeks- X^2=5.75, d.f.=4, p=0.12).

Table 3.2 Distance of male and female foxes from breeding dens for different cub age classes, combining data collected for all individuals of each sex (5 females and 6 males). Proximities are expressed as total number of and % (in parenthesis) of observations within given separation distances.

Cub age		*combined*	*distance from den*				
(weeks)	*sex*	*number of fixes*	0-100m	1-200m	2-300m	3-400m	400m+
0-2	F	20	1 (5.0)	4 (20.0)	2 (10.0)	2 (10.0)	11 (55.0)
2-4	F	37	3 (8.1)	4 (10.8)	2 (5.4)	9 (24.3)	19 (51.4)
4-6	F	30	7 (23.3)	3 (10.0)	5 (16.7)	6 (20.0)	10 (33.3)
6-8	F	28	6 (21.4)	3 (10.7)	5 (17.9)	1 (3.6)	13 (46.2)
8-10	F	37	10 (27.0)	4 (10.8)	4 (10.8)	4 (10.8)	15 (40.5)
10-12	F	29	9 (31.0)	3 (10.3)	1 (3.4)	1 (3.4)	15 (51.7)
12-14	F	18	3 (16.7)	5 (27.8)	2 (11.1)	1 (5.6)	7 (38.9)
0-2	M	28	5 (17.9)	6 (21.4)	5 (17.9)	2 (7.1)	10 (35.7)
2-4	M	44	21 (47.7)	5 (11.4)	7 (15.9)	8 (18.2)	3 (6.8)
4-6	M	39	18 (46.2)	8 (20.5)	8 (20.5)	3 (7.7)	2 (5.1)
6-8	M	33	10 (30.3)	7 (21.2)	7 (21.2)	2 (6.1)	7 (21.2)
8-10	M	37	13 (35.1)	10 (27.0)	6 (16.2)	2 (5.4)	6 (16.2)
10-12	M	36	13 (36.1)	9 (25.0)	3 (8.3)	3 (8.3)	8 (22.2)
12-14	M	31	8 (25.8)	4 (12.9)	10 (32.3)	3 (9.7)	6 (19.4)

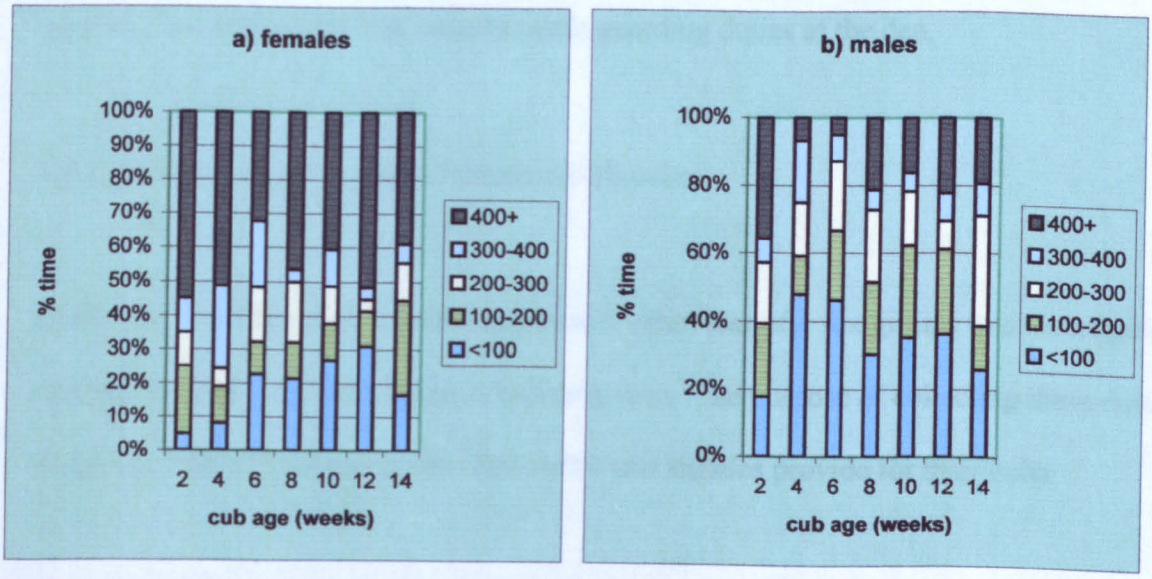

Figure 3.2 Proximity of a) females and b) males to breeding dens by cub age combining data for all individuals (5 females and 6 males).

How do mated partners co-ordinate their parental behaviour?

If mated partners alternate parental duties at breeding dens such that one partner stays at or near then den while the other forages further a field, we would expect that partners would be found together in the vicinity of breeding dens less often than would be expected by chance. Alternatively, if partners co-ordinate their behaviour such that they perform parental duties together, we would expect partners to be found together at breeding dens more often than would be expected by chance.

Observed frequencies of simultaneous male and female presence did not differ from those expected by chance for any of the 4 fox pairs (X^2 tests with 1 d.f., Ghost pair- X^2=0.06, N.S., Snorer pair- X^2=1.13, N.S., Astra pair- X^2=0.31, N.S., Puffadder pair- X^2=0.02, N.S.). This demonstrates that mated partners did not usually perform parental duties together, but neither did they strictly rotate guarding duties at the den.

3.3.2 Forms of care provided by males and females

During the 2002 breeding season the parental behaviour of 4 fox groups was investigated by directly observing adult foxes at breeding dens. The purpose of collecting these data was to establish the forms of care that males and females provide for their cubs.

Immediately prior to the onset of data collection the male of one fox pair was killed. This provided a natural experiment allowing an assessment of the parental tactics that a single

female would adopt. If den attendance increases offspring survivorship, we would predict that widowed females would adjust their behaviour in order to spend more time close to the den.

3.3.2.1 Proximities of males and females to breeding dens

Data on the proximity of the 3 fox pairs and single female fox to breeding dens, combined across observation sessions (and therefore cub age classes), are presented in Table 3.2 and Figure 3.2.

Visual inspection of Figure 3.3 again suggests substantial differences in the extent to which male and female foxes maintain proximity to breeding dens, with males spending significantly more time inside and close to breeding dens than females. Analysis confirms that, for all 3 fox pairs, differences between male and female partners were highly significant (All X^2 tests with 5 d.f.; Junction pair- $X^2=74.1$, $p<0.001$, What pair- $X^2=46.4$, $p<0.001$, Ghost pair- $X^2=58.9$, $p<0.001$).

The single female fox (ff74- Airstrip group) showed levels of den proximity apparently more similar to males than other females (Figure 3.3). Although den proximity of this fox differed significantly from all other individuals, her level of den proximity was more typical of males than females (compared with combined data of 3 males- $X^2=24.0$, d.f=5, $p<0.01$. Compared with combined female data- $X^2=101$, d.f=5, $p<0.001$). This suggests that the widowed female did adjust her behaviour in response to the absence of her

partner; spending more time at or inside her den, and being found more often in the vicinity of her den.

Ff 74 succeeded in raising at least one cub up to 6 weeks of age. After this left her territory and joined the neighbouring Ghost group- being found resting with the Ghost pair during the day and foraging with the (lactating) Ghost female at night. The fact that there was no increase in the number of cubs observed at the Ghost den (and no detectable discrepancy in cub size) suggests that ff74 did not successfully rear any cubs.

Patterns of male den attendance were similar to those calculated from radio-tracking data (c.p. Table and Figure 3.1 with Table and Figure 3.2), with males spending between 38.7 and 70 % of their time within 200m of breeding dens. Analysis again revealed significant inter-male differences in den attendance (X^2=61.6, d.f.=10, $p<0.001$). The 3 males observed did not, however, differ in the proportion of time they spent at or inside dens (X^2=0.95, d.f.=2, N.S.), but did differ in the proportion of time they were found at most other separation distances (All X^2 tests with 2 d.f.; 0-9m- X^2=14.1, $p<0.001$, 10-49m- X^2=16.4, $p<0.001$, 50-99m- X^2=0.7, N.S., 100-199m- X^2=14.1, $p<0.001$, 200m+- X^2=31.7, $p<0.001$).

By contrast, estimates of female den attendance were quite different from those calculated from radio-tracking data (Table & Figure 3.1) and through the observation of lactating females (Table 3.4), with females spending considerably less time close to dens. Given that data collected through the 2 other (more accurate) means produced similar

Table 3.3. The proportion of time that foxes were found within given distances from breeding dens. Data, from 3 pairs and one widowed female, is presented in terms of the number and percentage (in parenthesis) of observations within given separation distances. The number of observations sessions carried out for each fox pair, and cub age during each observation session are also given.

		N observation sessions	distances from den (% time)					
group	sex	(& cub age at each session)	inside/at	0-9	10-49	50-100	100-199	200+
Ghost	M	8 (4,4 ½,5,7,7 ½,9,10,10½)	35 (21.9)	1 (0.6)	4 (2.5)	6 (3.8)	16 (10)	98 (61.3)
	F	as above	0 (0)	0 (0)	0 (0)	4 (2.5)	0 (0)	156 (97.5)
Junction	M	6 (1 ½,2,3,4 ½,7,71/2)	21 (17.5)	10 (8.3)	16 (13.3)	7 (5.8)	30 (25)	36 (30)
F	as above		8 (6.7)	2 (1.7)	9 (7.5)	1 (0.8)	1 (0.8)	99 (82.5)
What	M	6 (1 ½,2½,3½,5,7,8)	26 (21.6)	1 (0.8)	4 (3.3)	5 (4.2)	12 (10)	72 (60)
	F	as above	0 (0)	0 (0)	0 (0)	0 (0)	7 (5.8)	113 (92.4)
Airstrip	F	3 (2,3,5)	7 (11.7)	0 (0)	0 (0)	6 (10)	21 (35)	26 (43.3)

(Data for foxes being at or inside dens was combined because it was often difficult to distinguish between these 2 categories. However, males were only visible at den entrances during only 17 of 82 records of this behaviour).

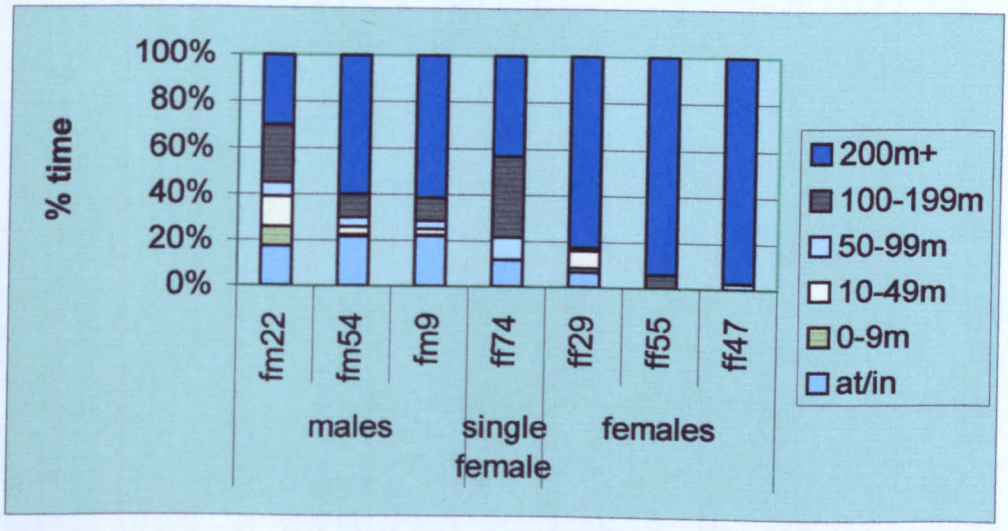

Figure 3.3 Proportion of time that 6 individual foxes spent at or close to breeding dens. Numbers of observation sessions per fox and cub age at each observation session are given in Table 3.2.

results (section 3.3.4), it is possible that the inaccuracy of technique employed to estimate proximity (judging distances by the strength of the radio-signal when animals could not be visually located) was responsible for this discrepancy. Alternatively, it is possible that our presence affected their behaviour.

3.3.2.2. Cub behaviour and forms of care provided by males and females

Observation of the behaviour of adult foxes and their cubs at breeding dens were also used to establish the forms of parental care provided by males and females. Box 3.1 lists forms of care observed or inferred to occur on the study site, and the evidence used to confirm their occurrence. Box 3.2 details key developments in cub behaviour, and states how these relate to the expression of parental care.

Box 3.1 Forms of parental care observed in study foxes, and evidence that they occurred.

*1) **Huddling**- Resting in contact with cubs to help them maintain their body temperature.*

Observed at den entrances, and inferred from fact that adults spend extended periods of time inside dens with cubs.

*2) **Grooming**- Grooming cubs to help remove ecto-parasites.*

Observed at den entrances.

*3) **Defending**- Active defence of den against cub predators.*

Males observed mobbing a black-backed jackals and an African wildcat that strayed close to dens.

*4) **Chaperoning**- Accompany cubs on foraging excursions in the vicinity of dens.*

Teaches cubs how to forage and provides them with access to solid food, while remaining vigilant for predators. Observed on numerous occasions.

*5) **Feeding**- Provisioning young at the den*

Adult foxes carry small birds, small mammals and large insects back to den. Established from observation of animal remains in den entrances (appendix 3.5), and inferred from behaviour of males, who foraged in the den vicinity and made short trips back to dens.

*6) **Carrying**- Carrying cubs between den sites.*

Foxes on the study site regularly switched den site, moving distances of up to 1km. Although this behaviour was not observed, when cubs were small and relatively immobile it is highly likely that they were carried by one or both of their parents.

Box 3.2 Stages of development in cub behaviour, and associated forms of parental care:

Cub behaviour	Cub age (weeks)	Evidence	Forms of care provided
emerge from dens	2 weeks	cubs seen at den entrance with adults during day and night (3 pairs)	1,2,3,6
take solid food	4 weeks	termites first appear in cub faeces (several dens)	1,2,3,4,5,6
foraging next to den	7 weeks	observed in Junction group	1,2,3,4,5,6
foraging >50m from den	9 weeks	observed in Ghost group	as above
foraging without adults	10 ½ weeks	observed in Ghost group	as above

3.3.3 Time budgets and parental behaviour of lactating females

During the 2001 breeding season, the time budgets and parental behaviour of lactating females were investigated through the direct observation of 3 females with pre-weaned cubs. The purpose of these data was to address the question of whether lactating females have time to provide direct care to their cubs. Three observations sessions were carried out on each female, one during each nocturnal time block.

Table 3.3 presents data on the time budgets of three lactating females. Figure 3.3 shows the average time budgets of the same three females during the pre-mating, mating, gestation and lactation periods.

On average the time budgets of lactating females were very similar to those of gestating females (Figure 3.3), with females spending approximately 40 % of their time walking and searching for food, and 45 % of their time feeding. Combining data for the three females, differences in gestation and lactation time budgets approach significant (X^2=8.86, d.f.=4, p=0.08). However, differences that did exist were a consequence of the fact that lactating females spent less time resting and more time guarding dens. If den guarding is included in the 'resting' rather than 'other' category then their combined time budgets are almost identical- X^2=0.79, d.f.=4, N.S.).

Figure 3.3 suggests that the time budgets of lactating females differ from those obtained during the pre-mating and mating periods, with lactating females spending more time actively foraging and less time resting. Statistical analysis confirms significant

Table 3.4 Time budgets of 3 lactating females. The table shows cub age during each observation session, the number (and %) of time female's were seen performing each activity, and the mean (& s.d.) Each female was followed 3 times, once during each time block.

			Behaviour (% time performing)					
Group	*ID*	*cub ages*	walk	search	feed	rest	at den	other
Astra	ff28	5,7,10	7 (18.4)	6 (15.8)	21 (55.3)	0 (0)	1 (2.6)	3 (7.9)
Junction	ff29	4,7,10	9 (22.0)	9 (22.0)	21 (51.2)	2 (4.9)	0 (0)	0 (0)
Snorer	ff16	6,8,11	7 (17.5)	6 (15.0)	11 (27.5)	2 (5.0)	10 (25.6)	3 (7.7)
		$\bar{x}$	19.5	17.8	44.9	3.4	8.1	5.2
		s.d.	2.38	3.83	15.0	2.86	14.1	4.5

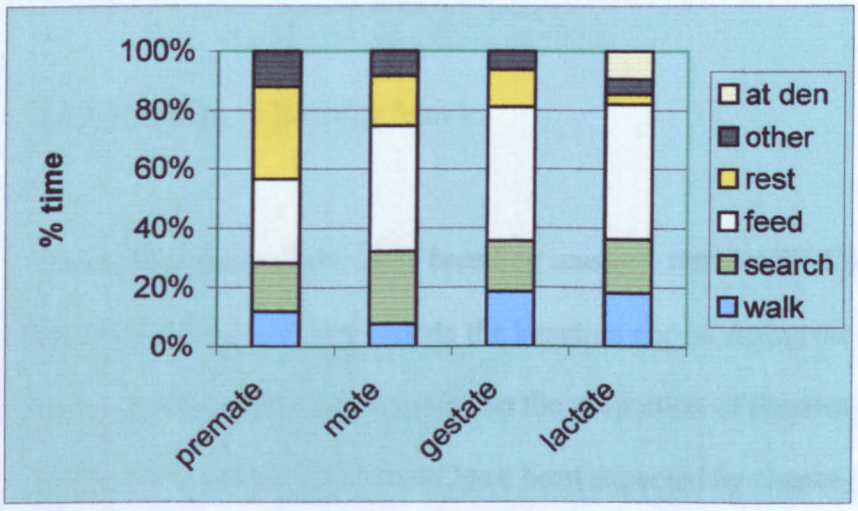

Figure 3.4 Average nocturnal time budgets of three females during pre-mating, mating, gestation and lactation. Females were followed 3 times during each phase (once during each time block).

differences, regardless of whether den guarding is considered as 'resting' (versus pre-mating- X^2=39.9, d.f.=4, $p<0.01$, versus mating- X^2=23.3, d.f.=4, $p<0.01$) or 'other' behaviour (versus pre-mating- X^2=18.9, d.f.=4, $p<0.01$, versus mating- X^2=12.4, d.f.=4, $p<0.02$).

The data confirm that lactating females have very little time available to spend in the direct care of cubs. The data also reveal that females forage at close to maximum rate throughout the gestation as well as lactation.

Data on proximities of lactating females to breeding dens are presented in appendix 3.4. The combined den proximity data from these females did not differ from combined radio-tracking data (presented in the previous section) for these (X^2=3.57, d.f.=4, N.S.) or for all females (X^2=8.64, d.f.=4, N.S.). This suggests that telemetry data provided an accurate assessment of the amount of time lactating females spent close to breeding dens.

3.3.4 Mortality of lactating females

During the course of the 2001 breeding season 4 females died during lactation. By contrast, no females died outside the lactation period during the entire course of the study. Statistical analysis reveals that the proportion of females dying during lactation is significantly greater than would have been expected by chance (X^2 test with 1 d.f., expected number of females dying during and outside lactation calculated by multiplying

the number of females that died by proportion of the year that females spend inside and outside lactation- X^2=9.91, p<0.01).

Comparison of the territory quality of females that died with those that survived revealed that, for 3 of the 5 measures of territory quality, these females occupied significantly lower quality ranges (2-tailed t-tests- MCP range sizes t=-3.14, d.f.=8, p=0.01, Kernel range size- t=-1.51, d.f.=8, p=0.16, termite density- t=-1.96, d.f.=8, p=0.04 , MCP holes- t=-3.00, d.f.=8, p=0.005, Kernel holes- t=-2.01, d.f.=8, p=0.06).

3.3.5 Effects of male care and territory quality on reproductive success

The relationship between male den attendance, territory quality and different measures of reproductive success were investigated to determine the extent to which male care and resource availability effect reproductive success. Details the reproductive events included in these analyses are presented in Table 3.5.

Does territory quality affect initial litter size, or measures of reproductive success?

None of the 5 measures of territory quality was significantly related to the number of cubs first seen (univariate regressions: termite density- F 1,12=1, p=0.34, MCP range- F1,12=2.52, p=0.14, Kernel range- F1,12=2.14, p=0.17, MCP holes- F1,12=2.61, p=0.13, Kernel holes- F1,12=2.77, p=0.34), suggesting litter size at or close to birth is not related to territory quality.

Table 3.5 Dates and success of all breeding attempts by fox groups on the study site monitored during 2001 and 2002. The Table presents data on number of cubs born (maximum number seen or captured), and the number and proportion of cubs reaching 14 weeks and 6 months of age. Where success is 0, the reason for breeding failure is given.

Group	Year	Date	no. cubs born	number (and proportion) reaching 14 weeks	6 months	cause of failure
Astra	2001	12-Sep	4	3 (0.75)	3 (0.75)	-
Ghost	2001	18-Aug	3	3 (1)	2 (0.67)	-
	2002	15-Aug	3	2 (0.67)	?	-
What	2001	18-Sep	4	2 (0.5)	1 (0.25)	-
	2002	24-Aug	4	3 (0.75)	?	-
Reflector	2001	1-Feb	?	0 (0)	0 (0)	female killed
Junction	2001	20-Sep	4	4 (1)	3 (0.75)	-
	2002	10-Sep	4	4 (1)	?	-
Grebe	2001	1-Sep	5	0 (0)	0 (0)	female killed
Neils	2001	22-Aug	5	5 (1)	4 (0.8)	-
Mzee	2001	15-Sep	5	4 (0.8)	4 (0.8)	-
Snorer	2001	1-Sep	3	3 (1)	2 (0.67)	-
Everest	2001	5-Feb	3	0 (0)	0 (0)	female killed
		16-Sep	4	3 (0.75)	3 (0.75)	-
Puffadder	2001	1-Sep	3	3 (1)	1 (0.33)	-
Camp	2001	8-Sep	3	0 (0)	0 (0)	female killed

Measures of territory quality did, however, relate to all estimates of reproductive success;

Four out of the five measures of territory quality were significantly associated with the number of offspring surviving to weaning, and the 5th measure was close to being significant (single regressions; termite density- $F_{1,14}=6.19$, $p=0.03$, MCP range- $F_{1,14}=15.2$, $p=0.002$, Kernel range- $F_{1,14}=4.17$, $p=0.06$, MCP holes- $F_{1,14}=11.1$, $p=0.01$, Kernel holes- $F_{1,14}=5.55$, $p=0.03$). Two measures of territory quality were significantly related the proportion of cubs surviving from birth to 14 weeks, and one approached significance (single regressions; termite density- $F_{1,14}=4.02$, $p=0.06$, MCP range- $F_{1,14}=7.62$, $p=0.02$, Kernel range- $F_{1,14}=1.89$, $p=0.19$, MCP holes- $F_{1,14}=5.09$, $p=0.04$, Kernel holes- $F_{1,14}=2.57$, $p=0.13$).

All five measures of territory quality were significantly related to the number of cubs reaching dispersal age (single regressions; termite density- $F_{1,11}=13.1$, $p=0.004$, MCP range- $F_{1,11}=13.3$, $p=0.003$, Kernel range- $F_{1,11}=4.68$, $p=0.05$, MCP holes- $F_{1,14}=11.1$, $p=0.01$, Kernel holes- $F_{1,11}=7.25$, $p=0.02$). Two of the five measures of territory quality had significant effects on the proportion of cubs surviving from birth to dispersal, and two further measures approached significance (single regressions; termite density- $F_{1,11}=4.57$, $p=0.06$, MCP range- $F_{1,11}=7.55$, $p=0.02$, Kernel range- $F_{1,11}=2.49$, $p=0.14$, MCP holes- $F_{1,11}=5.77$, $p=0.04$, Kernel holes- $F_{1,11}=3.67$, $p=0.08$).

These results demonstrate that reproductive success consistently correlates with measures of home range quality. Two measures of territory quality, MCP range size and total termite abundance on MCP territories, correlated with all measures of reproductive success. This suggests that these measurements provided the best estimation of territory quality.

Why does territory quality affect reproductive success?

Four females died during the course of lactation, and their partners failed to raise any cubs (Table 3.5). Data presented in section 3.3.4 showed that these females occupied lower quality territories than females that survived lactation. It is possible, therefore, that the association between territory quality and reproductive success was solely a consequence of the increased mortality of females on lower quality territories.

With dead females removed from the data set, three measures of territory quality were significantly associated with initial litter size (single regressions; termite density- $F_{1,10}=1.86$, $p=0.2$, MCP range- $F_{1,10}=8.07$, $p=0.02$, Kernel range- $F_{1,10}=4.42$, $p=0.06$, MCP holes- $F_{1,10}=4.97$, $p=0.05$, Kernel holes- $F_{1,10}=5$, $p=0.05$). This association did not exist across the complete data set, and there is no obvious reason why it did so after the reproductive attempts of dead females were excluded from the analysis.

Four measures of territory quality associated with the number of cubs reaching 14 weeks (single regressions; termite density- $F_{1,10}=6.43$, $p=0.03$, MCP range- $F_{1,10}=6$, $p=0.03$,

Kernel range- F 1,10=4.42, p=0.06, MCP holes- F 1,10=7.43, p=0.02, Kernel holes- F 1,10=4.93, p=0.05), but no measures were significantly related to the proportion of cubs surviving to 14 weeks (single regressions; termite density- F 1,10=4.43, p=0.06, MCP range- F 1,10=0.76, p=0.4, Kernel range- F 1,10=0.64, p=0.44, MCP holes- F 1,10=2.15, p=0.17, Kernel holes- F 1,10=1.12, p=0.3).

No measures of territory quality where significantly related to the number of cubs reaching dispersal, although several measures approached significance, and sample sizes were small (single regressions; termite density- F 1,7=2.52, p=0.16, MCP range- F 1,7=0.76, p=0.1, Kernel range- F 1,7=3.77, p=0.09, MCP holes- F 1,7=3.86, p=0.09, Kernel holes- F 1,7=4.05, p=0.08).

Is male den attendance related to initial litter size or territory quality, and does it affect reproductive success?

Analysis reveals that male den attendance is not related to initial litter size (F 1,9 =0.08, p=0.74, % time within 100m of the den- F 1,9=1.7, p=0.22). Den attendance did, however, relate significantly to 4 of the 5 measures of territory quality (termite density- F 1,9=6.19, p=0.03, MCP range- F 1,14=15.2, p=0.002, Kernel range- F 1,14=4.17, p=0.06, MCP holes- F 1,14=11.1, p=0.01, Kernel holes- F 1,14=5.55, p=0.03), with males on high quality territories spending significantly more time close to breeding dens.

The relationship between male den attendance and the number of cubs reaching 14 weeks approached significance ($F_{1,9}=4.30$, $p=0.08$), and male den attendance was significantly associated with the proportion of cubs surviving to 14 weeks ($F_{1,9}=7.76$, $p=0.02$). Neither the number ($F_{1,6}=0.4$, $p=0.55$) nor proportion ($F_{1,6}=0.59$, $p=0.47$) of cubs surviving to dispersal age related to male den attendance, although sample sizes in these analyses were small ($n=8$).

The relative effects of male care and territory quality on cub survival

Because measures of territory quality and male den attendance both related significantly to some measures of reproductive success, multiple regressions were carried out to establish their relative effects. 11 breeding events were included in these analyses.

Male den attendance and MCP territory size together explained a significant amount of variation in the number of cubs weaned ($F_{2,8}=6.57$, $p=0.02$). However, only MCP territory size accounted for significant amount of this variation (see Figure 3.5; t-tests for significance of partial regression co-efficient; MCP territory size- $t=2.56$, $p=0.03$, den attendance- $t=0.26$, $p=0.8$).

Male den attendance and MCP range size together explained a significant amount of variation in the proportion of cubs surviving from birth to weaning ($F_{2,8}=5.52$, $p=0.03$). However, neither factor alone explained a significant amount of variation (MCP range size- $t=1.47$, $p=0.18$, den attendance- $t=1.29$, $p=0.23$). The data set used in this analysis

includes one breeding attempt that failed after the lactating female died. Because the death of females always resulted in reproductive failure (Table 3.5), it could be argued that cub survival in this group was unrelated to male den attendance. With this female removed from the data set male den attendance and MCP range size again explain a significant amount of variation in the proportion of cubs surviving from birth to weaning ($F_{2,8}=5.52$, $p=0.03$). However, male den attendance now explains a significant proportion of this variation, whereas territory size does not (see Figure 3.6; den attendance- $t=2.96$, $p=0.02$, range size- $t=-0.36$, $p=0.73$).

Although the relative effects of den attendance are difficult to disentangle (because they are inter-correlated), the results suggest that both variables have a significant affect on reproductive success.

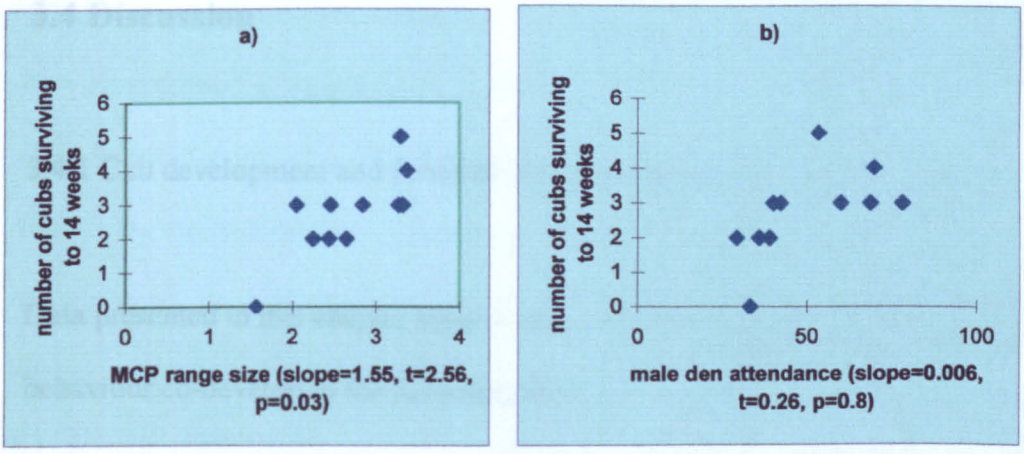

Figure 3.5 relative effects of a) territory size and b) male den attendance on the number of cubs surviving to 14 weeks (for 11 breeding events)

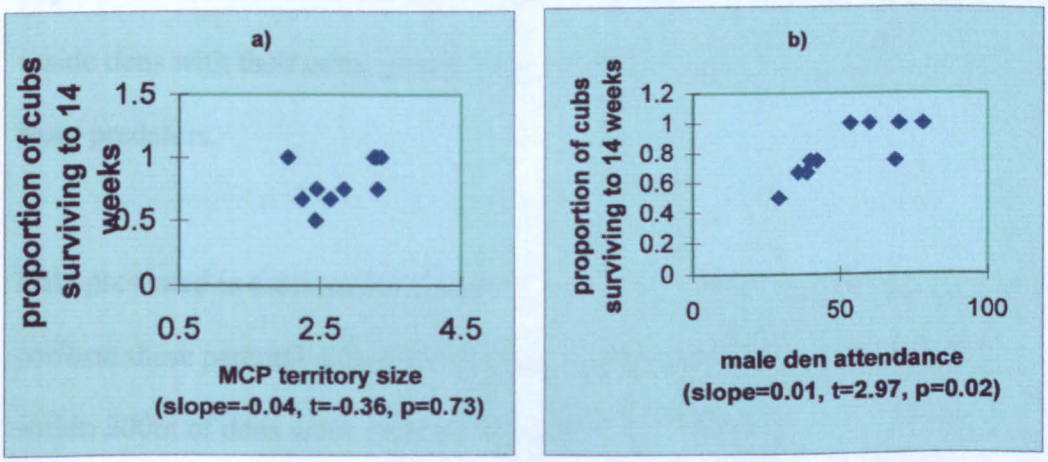

Figure 3.6 relative effects of a) territory size and b) male den attendance on the proportion of cubs surviving to 14 weeks (for 10 breeding events).

3.4 Discussion

3.4.1 Cub development and forms of care provided by males and females

Data presented in this chapter suggest that cub behaviour, and paternal and maternal behaviour co-develop in the following way: -

For the first 2 weeks of their lives, bat-eared fox cubs remain inside dens. They first appear at den entrances at 2 weeks, but for at least a further 2 weeks they do not venture beyond the den entrance. During the first 4 weeks of their cubs' lives adult foxes rest inside dens with their cubs, groom cubs, guard den entrances and actively defend cubs from predators.

Data presented in sections 3.3.1 and 3.3.2 show that that it is primarily males who perform these parental duties. On average, males spend approximately 40% of their time within 200m of dens when cubs are aged between 0 and 2 weeks, and 60% of their time within 200m of their dens when cubs are aged between 2 and 4 weeks (Table 3.2). At least 20 % of this time appears to be spent inside dens or at den entrances (Table 3.3). The remainder of the time that males are within 200m of dens they apparently forage (when males could not be seen their radio-signals suggested they were constantly moving).

The presence of indigestible termite heads in cub faeces shows that, by 4 weeks of age, they have started to take solid food. Although cubs were not observed foraging outside dens before 7 weeks, it is likely that these termites were consumed during short foraging trips in the immediate den vicinity. The presence of cub tracks prove that some cubs were moving up to 5m from dens by 4 weeks, and a majority of dens (35 of 51) were inside or within 5m of termite mounds. This said, it is possible that some initial foraging by cubs took place inside dens (underground).

Initial foraging trips made by cubs were short in duration (between 10 and 30 minutes) and confined to the immediate den vicinity. Consequently, between the ages of 4 and 8 weeks, cubs still spent the majority of their time inside dens (cubs were only outside dens during 2 of the 8 observation sessions carried out between these cub ages). Initially, the male or both adults always accompanied foraging cubs. Adult chaperones probably played a role in teaching cubs how to forage, as well as remaining vigilant and alerting cubs to presence of potential predators (see also Pauw 2000). Adults may also call cubs from dens when termites are active nearby; because termites spend considerable amount of time underground it is probably not worth cubs foraging unless termites are active in the immediate vicinity.

As cubs increase in age they began to forage further from their dens (still in the company of an adult chaperone), and spent increasing amounts of time outside the den (cubs were observed during 3 of 4 observation sessions carried out when cubs were between 8 and 12 weeks of age). By 9 weeks cubs were seen up to 50 m from the den, and by 10 weeks

they foraged up to 100 m from the den. At 10 ½ weeks of age cubs were first seen foraging alone in the den vicinity. When cubs are aged between 12 and 14 weeks, the proportion of time males and females spend within 100 m of dens drops (Figure 3.2). This is probably a reflection of the fact that, by this age, cubs are regularly foraging more than 100m from their dens.

In addition to accompanying cubs on foraging trips, adults also bring some items of food back to dens. On several occasions remains of small mammals, birds and large insects were found inside den entrances (appendix 3.5). The fact that males foraged in the vicinity of dens (Table 3.3), and made short trips back to den sites, suggests that they were primarily or entirely responsible for bringing food back to cubs.

When cubs are between 4 and 12 weeks of age, males spend more time close to breeding dens than females (on average approximately 60 % of their time is spent within 200m of breeding dens- Figure 3.2). This, and observational data presented in Table 3.3, confirms that between these ages males were primarily responsible for direct cub care. Having said this, females spend increasing amount of time near dens as cub age increases (Table 3.2). By the time cubs reach 12 weeks of age the roles of males and females, at least in terms of the proportion of time spent near dens, are similar.

After bat-eared fox cubs were weaned (at 14 weeks), they spent approximately 20 weeks on their natal territories before dispersing at between 7 and 8 months of age (data from 8 groups with cubs that reached dispersal age). Incidental observations of fox groups made

during this period show that families remain together as cohesive units that usually rest together during the day and forage together at night (appendix 3.6). During this time cubs probably continue benefiting from their parents close presence.

3.4.2 Comparison with data on bat-eared fox parental behaviour from other studies

The parental roles of bat-eared foxes on the study site were largely similar to those observed by Lampecht (1979) and Maas (1992- both in the Serengeti), Malcolm (1986- in the Masai Mara) and Pauw (2000- in the Kalahari). All of these studies report that males are primarily responsible for the direct care of cubs (guarding, grooming, huddling and accompanying cubs on foraging trips), while females spend the majority of their time foraging away from the dens.

The direct provisioning of cubs observed in this study has previously only been described by Pauw (2000, who witnessed an adult male, and to a lesser extent his partner, carrying semi-chewed lizards back to the den). Like Pauw, I suggest that cub provisioning requires an alteration of normal foraging behaviour, because foxes were never observed attempting to catch vertebrate prey outside of the breeding season (during more than 115 hours of observation). Male regurgitation of food to females and cubs was not observed in this study, but has been observed by Lamprecht (1979; but even in his study it was unusual).

In this study adults were not observed carrying cubs between den sites, but frequent den switching by families with young cubs suggests that this must have occurred. Maas (1992), Malcolm (1986) and Pauw (2000) all report that males and females both perform this parental duty. Similarly, although den construction was only observed once on the study site (by a male), Pauw states that both sexes perform this duty.

While the forms of paternal care observed on the study site were similar to those observed elsewhere, there is some evidence to suggest that the amount of care males provides differs between populations. For example Maas (1992) found that, when cubs are aged between 0 and 9 weeks, males spend almost 90% of their time within 50m of dens. It is possible that these behavioural differences stem from differences in diet, as Maas' foxes fed on Hodotermes termites, which are apparently the species preferred food.

3.4.3 Female investment in reproduction

Data presented in this chapter suggest that reproduction subjects female bat-eared foxes to enormous nutritional stress. Not only did activity rates of gestating and lactating differ from those of non-breeding foxes (section 3.3), but females also suffered increased mortality, with females on low quality territories being most likely to die during lactation (section 3.4). Previous mammalian studies have demonstrated similar effects; for example Clutton-Brock *et al.* 1982, Dunbar & Dunbar 1988 & Koenig *et al.* 1997 have all shown that non-lactating females spend more time feeding than non-lactating females.

Several studies have reported increased mortality of lactating females (see Neuhaus & Pelletier 2001), but to my knowledge no previous studies have been able to specifically relate female mortality to territory quality. While it is not entirely clear why lactating females suffered increased mortality, observation of their behaviour, and the discovery of fresh carcasses suggest that their intense focus on foraging (alone) renders them highly susceptible to predation.

Lactation is assumed to be the most energetically costly stage of reproduction (Clutton-brock *et al.* 1989, Oftedahl & Gittleman 1989). It has been estimated that, under some circumstances, lactating females must increase food intake two fold just to maintain normal body weight (Randolph *et al.* 1977, Oftedahl & Gittleman 1989). This is probably impossible for bat-eared foxes, as they spend approximately 60% of their time foraging outside of the breeding season. As a result lactating females probably rely on fat reserves stored prior to parturition. This is suggested by the fact that female foxes increase their feeding rate during the mating period, and feed at close to maximum rate throughout gestation.

Moehlman (1989) has argued that female bat-eared foxes huge investment in reproduction decreases the requirement for male care. Data presented in this chapter suggest that the opposite may be true. Because lactating females have little or no time available to spend huddling, grooming, guarding and chaperoning foraging cubs, male care becomes all the more important.

3.4.4 Effects of male care and territory quality on breeding success

The importance of male care is confirmed by the fact that, even after controlling for effects of territory quality, male den attendance significantly affected reproductive success (the proportion of cubs surviving to 14 weeks). This has never previously been demonstrated in any study of a wild canid, and has only once been demonstrated in a natural population of mammals (Gubernick & Teferi 2000). The result is consistent with the observation that widowed females appear to adjust their behaviour in order to spend more time close to dens (this study and Maas 1993); because this behavioural adjustment probably decreased foraging time (and therefore milk production) it seems likely that it must have a compensatory benefit.

Given that male den attendance significantly affects cub survival, it is tempting to ask why there is so much inter-individual variation in this den attendance (section 3.3.1)? The most likely explanation for this is that males adjust their level of care according to variation in its costs to themselves, and benefit to their offspring (Winkler 1987). This is suggested by the fact that male den attendance is positively associated with territory quality (section 3.3.5). Den attendance is likely to carry a substantial energetic cost (e.g. Clutton-Brock *et al.* 1998), which males on lower quality territories may have been unable to meet (Wittenberger 1979, Carlisle 1982). Additionally, if females on better quality territories are able to invest more in offspring, benefits of male investment in

offspring may also increase (as the benefits of male investment are expected to increase with litter size- Lazarus & Inglis 1986).

Data presented in this chapter also reveal that territory quality affected most measures of reproductive success. Part of reason for this was that females on lower quality territories were more likely to die during lactation. However, even with these female removed from the data set, associations between some measures of territory quality and reproductive success remained significant. Territory quality significantly affected the number of cubs surviving to 14 weeks, even after controlling for the effect of male care. Similarly, Maas (1993) reported a positive association between litter size and termite abundance, and demonstrated that females on higher quality territories spend more time suckling cubs.

3.4.5 Implications for the maintenance of social and genetic monogamy

Would males do better dividing their care between litters?

Males spent an average of 56 % of their time, and a maximum of 78.4 % of the time within 200m of dens of their dens. Assuming a 10% travel time between dispersed dens (or 6 single trips between dens 1 km apart, based on foxes maximum observed travelling speed), a male dividing care between 2 dens would spend an average of 23 %, or a maximum of 34.2 % of his time at each den. Results of the multiple regression analysis (Figure 3.6) suggest that this would reduce the proportion of each litter surviving from 0.8 to 0.5, and from 1.0 to 0.65. Consequently, dividing care between 2 litters would

increase male reproductive success by 20% (for average levels of den attendance) to 30% (for maximum observed levels of den attendance).

This analysis, however, only considers the adaptive effect of nocturnal den attendance during the first 14 weeks of cub life. Since pup survival is also likely to be increased by diurnal den guarding (appendix 3.2) and post-weaning cub care (appendix 3.6), it is uncertain whether males dividing care equally between dispersed litters would substantially increase their reproductive success.

By contrast, because at least some forms of care provided by males are non-depreciable (guarding, chaperoning and to a lesser extent huddling), it seems likely that males could increase their reproductive success by dividing their care between multiple litters housed in a communal den. This is supported by Maas' (1993) observation that males in communal dens enjoyed greater reproductive success than males breeding in monogamous pairs. However, males are almost certainly not in a position to be able to force females to den communally.

Should female always avoid polygyny?

Davies (1989) points out that is difficult to make predictions about whether females should accept or avoid polygyny, because this requires knowledge of variation in male territory quality, the degree to which sharing a territory (and male care) affect female

reproductive success, and the extent to which females are free to choose where they settle. Nonetheless, data presented in this chapter shed some light on this issue: -

The fact that male den attendance increases cub survival confirms that there would be a cost to females sharing male care. This cost would be greatest for females with litters housed in separate dens (see above), but would also exist for litters housed in communal dens (since some forms of care provided by males, including provisioning, grooming and carrying cubs between dens, are depreciable; see Kleiman & Malcolm 1981).

Because territory quality (as measured by size) also had a significant effect on reproductive success, it is possible that the best mating option for some unpaired females would be to join mated pairs on high quality territories (and share male care). However, without knowing the extent to which sharing a territory would reduce a female's access to food, it is difficult to know whether this would be the case (see above). What is more certain is that resident females would almost certainly gain by excluding unrelated females from their territories. Thus aggression by 'paired females' could well be a factor preventing the formation of 'unrelated' polygynous groups.

Data from Maas (1993) confirms that polygyny reduces the reproductive success of female bat-eared foxes. Although the litter sizes of polygynous groups (sharing a communal den) were greater than that those of monogamous pairs, the average number of cubs per female was lower. While this may have resulted from factors other than a reduction (per cub) in male care, such as reduced (per female) access to food or inter-

litter competition at the teat (see Manning *et al.* 1995), it confirms that polygyny is unlikely to be favoured option of resident females unless additional females are relatives (so that resident females accrue indirect fitness benefits).

Potential costs of infidelity

Under certain conditions, males are expected to facultatively adjust levels of paternal investment according to their confidence of paternity (section 3.1.4). While it is not clear if these conditions exist in the bat-eared fox, the fact that male care enhances offspring survival suggests that infidelity carries a potentially high cost to females.

3.4.6 Summary

Social monogamy may have evolved or be maintained because paternal care is required for successful reproduction (Wittenberger & Tilson 1980). This hypothesis has been assumed to apply to canids, because canid males usually provide assistance to breeding females (Kleiman 1977). The expression of (and requirement for) male care may also relate to the degree of sexual fidelity in socially monogamous species, because males should be under strong selective pressure not to invest in offspring that they have not fathered (Trivers 1972).

In order to understand the role that paternal care plays in favouring evolution and maintenance of monogamy, and promoting sexual fidelity, it is necessary to establish whether, and to what degree, male assistance is necessary for successful reproduction.

Very few data are available on this subject for mammals (Gubernick & Teferi 2000), and no data are available for any species of canid.

Moehlman (1989) has suggested that because bat-eared fox females invest heavily in reproduction male care might not be required for successful breeding. Data presented in this chapter confirm that females invest heavily in reproduction, with females feeding at close to maximum rate throughout gestation and lactation, and suffering increased mortality during lactation. Contrary to the view of Moehlman (1989) however, I suggest that the huge reproductive investment of females' leaves them with very little time to spend directly caring for cubs, and makes males' involvement in cub care all the more important. This conclusion is strongly supported by the fact that males were heavily involved in many aspects of cub care, and that male care (den attendance) significantly correlated with cub survival.

Because sharing beneficial male care would be costly for females, it is likely that they are under selective pressure to avoid polygyny. The situation for males is less clear and it is possible that, despite the fact that paternal care enhances offspring survival, males could increase their reproductive success by dividing care between the litters of more than one female.

Chapter 4

The spatial and temporal distribution of fertile females, and the distribution of resources on male territories- implications for the maintenance of social monogamy

4.1 Introduction

4.1.1 Could the requirement for paternal care alone have promoted the evolution of monogamy?

Several authors have proposed that monogamy has evolved because male care is essential for offspring survival (Kleiman 1967, 1977, Moehlman 1986, Gubernick *et al.* 1993, Runcie 2000). However, the observation that male care enhances offspring survival in contemporary populations (chapter 3, Gubernick & Teferi 2000) does not prove that the requirement for paternal was a factor favouring the initial evolution of monogamy, or indeed that it is the only factor favouring the maintenance of monogamy (see chapter 3).

Clutton-Brock and Harvey (1978) pointed out that 'the difficulty with explaining monogamy as a consequence of the need for paternal care is that paternal care is likely to have evolved in circumstances in which polygyny is prevented by other factors'. In other words, after the initial evolution of the pair bond, when males have potential to provide

beneficial care for offspring (which they may not always have, see Dunbar 1988) we would expect the expression and requirement of male care to co-evolve. As a result, information about the adaptive significance of paternal care in contemporary breeding systems may provide little indication of the original requirement for male assistance (Clutton-Brock 1991).

In addition to this, there are theoretical reasons for believing that a requirement for male care is unlikely to have evolved prior to its expression. These centre on the fact that females producing litters *requiring* male help (prior to the evolution of male care) would suffer an unnecessary cost. In this context, Dunbar (1995) produced a model examining the circumstances under which twinning could have evolved from single offspring births in the Callitrichids (marmosets and tamarins). Because females producing twins (in the absence of male assistance) suffer a high cost, and because single offspring do not benefit significantly from male assistance, Dunbar concluded that 'it seems implausible to invoke a males help in caring for growing infants to explain the evolution of monogamy'.

This argument does not necessarily rule out a role for male care in the initial evolution of monogamy, because it is possible to imagine some female birthing strategies providing a *potential* for beneficial male assistance (without carrying this cost) prior to the evolution of male care (for example if females already produced larger litters of smaller offspring, as canids do). Additionally, it is possible that the requirement for male care promoted the evolution of social monogamy from mating systems in which male care was already expressed. This seems unlikely, however, because there are very few non-monogamous

species in which males provide care for their offspring (Woodroffe & Vincent 1994; although this may have occurred in the rodents- see Gubernick & Teferi 2000, Komers & Brotherton 1997).

4.1.2 Female spatial distribution and the evolution of monogamy

The observation that social monogamy often occurs in the absence of male care (mammals, Komers 1996, Kishimoto & Kawamichi 1996, FitzGibbon 1997; fish, Morley & Balshine 2002; reptiles, Gillette *et al.* 2000) proves that in many cases, factors other than a requirement of paternal assistance must have promoted its evolution. Additionally, arguments presented in the previous section suggest that even where males do provide care for offspring, other factors may (or in some cases must) have promoted the initial evolution of monogamy. So why then has monogamy evolved?

Several theories have attempted to explain mammalian monogamy in terms of female distribution. In particular monogamy has been proposed to evolve when females are solitary and too highly dispersed to make polygyny possible (-the 'over-dispersion hypothesis' Emlen & Oring 1977, Wickler & Seibt 1983, Cockburn 1988). Some authors have specifically suggested that male may be incapable of defending the resources required by more than one female (Murray 1984, Gosling 1986). Empirical data, however, suggests that this hypothesis does not explain the occurrence of monogamy in rodents, primates or ungulates: -

Dunbar (1988) and Cockburn (1988) have shown that there is no association between female home range size and monogamy in primates and rodents respectively. Dunbar further calculated that most monogamous male primates could readily defend ranges large enough to sustain the nutritional requirements of 4 or 5 females. Similarly, Brotherton & Manser (1997) demonstrated that monogamous male dik-diks can and often do defend territories with sufficient resources to support two or more females.

4.1.3 Monogamy as a mate guarding strategy

Komers & Brotherton (1997), in a comparative study, investigated the relative importance of female dispersion and the requirement for male care as factors favouring the evolution of mammalian monogamy. They found that, among mammals, monogamy has evolved significantly more often in the absence of paternal care than in it's presence. Surprisingly though, they also found that monogamy has evolved most often where females occupy small, rather than large, exclusive ranges. In light of this result Komers & Brotherton (1997) suggest that monogamy may have evolved because the long-term defence of single females must often be advantageous to males.

Although this 'mate-guarding' hypothesis for the evolution of monogamy has not been explicitly defined, it implies that the rate of successful mating by monogamous males (per unit time) is greater than that of males adopting alternative reproductive strategies. Studies of socially monogamous species from several taxa support the notion that males

may be monogamous for this reason (mammals- Brotherton & Manser 1997, FitzGibbon 1997; reptiles- Bull et al. 1998; crustaceans- Mathews 2003).

There are several other reasons why the exclusive defence of a single female (monogamy) could increase male lifetime reproductive success. In particular this strategy might reduce energy expenditure or predation risk and thus result in a increased reproductive life span (Kishomoto & Kawamichi 1996, FitzGibbon 1997).

4.1.4 Breeding synchrony and it's effects on male mating behaviour

The ability of males to monopolize fertile females has been predicted to depend crucially on the distribution of receptive females in time as well as space (Emlen & Oring 1977). When females are widely distributed in space (i.e. not social) and their oestrous periods are highly synchronized, it may be difficult or impossible for males to defend more than one receptive female. Conversely, when females are spatially clumped and their receptive periods are not synchronized, males have the greatest opportunity to monopolize access to them (Ims 1989, Eberle & Kappeler 2002). Although not considered in the analysis of Komers & Brotherton (1997- see previous section), it is possible that, in some taxa at least, female breeding synchrony may have been a factor promoting the evolution of monogamy.

Related to this possibility, two recent studies of polygynous carnivore species have convincingly demonstrated that increasing synchrony of female oestrus reduces the

ability of the most competitive males to monopolise fertile females. Gehrt & Fritzell (1999), working on Racoons, demonstrated that as female oestrous synchrony increased so did subordinate males' access to oestrous females. Similarly, Say *et al.* (2001) demonstrated that when domestic cats bred synchronously, dominant males sired 4 times fewer offspring than when they bred asynchronously.

4.1.5 Investigating the costs and benefits of social monogamy

Investigating the costs and benefits associated with different mating strategies (like monogamy and polygyny) can be problematic. Where individuals in one population employ different mating strategies, data can be collected to directly compare their relative advantages and disadvantages (e.g. Kishomoto & Kawamichi 1996). Additionally, if mating behaviour varies between populations or seasons, equivalent comparisons can be made (e.g. Zabel & Taggart 1989).

An alternative (indirect) way of shedding light on the costs and benefits of social monogamy is through the observation of individuals that lose their partners (either naturally or experimentally- e.g. FitzGibbon 1997). The fate of widowed animals can help determine whether males and females compete primarily for partners or territories, and the intensity with which they compete for these resources (Morley & Balshine 2002). This information can be used to make predictions about whether males or females are likely to be capable of pursuing alternative reproductive strategies.

4.1.6 Spatial organization, breeding synchrony and the oestrous cycles of female canids

Numerous field studies on Canids have provided detailed information on spatial organisation. Almost all of these report that adult females (and mated pairs) occupy largely exclusive home ranges, with a minimal degree of overlap between neighbours (Kit fox- 8.3 % of female MCP ranges, White & Ralls 1993; Blanford's fox- 7.4 % of female 80% minimum polygon ranges, Geffen & Macdonald 1992; Arctic fox- 2.9% of pairs outer convex polygon ranges, Stand *et al.* 1998; Crab-eating fox- 3.5% overlap of female restricted polygons ranges, Macdonald & Courtenay 1996; Black-backed and Golden Jackal- Moehlman 1983).

Although little detailed data on breeding synchrony is available, the majority of Canid species (with the exception of the bush dog, Christie & Bell 1971, cited in Asa & Valdespino 1998; and African wild dog, Malcolm & Marten 1982) also have restricted annual breeding seasons that often correspond to cycles of seasonal rainfall and food availability (Kleiman 1967, Asa & Valdespino 1998).

An unusual feature of Canid reproductive biology is that most species mono-oestrous (they have only one oestrous cycle per year), and relative to other mammals, stages of the ovulatory cycle are substantially prolonged (Asa & Valdespino 1998). Pro-oestrus, which may be advertised by a blood tinged uterine discharge, can begin up to six weeks prior to oestrus (in wolves- Asa *et al.* 1986; in the genus Canis- Kleiman 1968, in Black-backed Jackals, van der Merve 1953), and is often accompanied by an increased rate of urine

marking (by both sexes) and behavioural coordination of mated partners (wolves, Asa *et al.* 1990; golden jackals- Golani & Mendelssohn 1971; bat-eared foxes, see chapter 5). Oestrus itself is also prolonged, and can last for between 5 to10 days (Golani & Mendelssohn 1971, Rosenburg 1971, Asa *et al.* 1986), during which time partners copulate repeatedly. This is considerably longer than the single day of oestrus typical of most other mammal species (Asa & Valdespino 1998).

4.1.7 Effects of female oestrus characteristics on male mating options

The nature of female oestrus is predicted to influence male reproductive tactics. Gomendio *et al.* (1998) have stated that extended mate guarding (and repeated copulation) should be favoured when oestrus is spontaneous, oestrous periods are long and males are unable to pinpoint the precise timing of ovulation (all of which apply to Canids). In Canids, female advertisement of oestrus (and pro-estrus, through increased rate of urine marking) may further increase the necessity for prolonged mate guarding, because fertile females should be relatively easy for intruding males to detect. It seems likely that, in order to ensure paternity, male Canids may be obliged to remain close to oestrous females for extended lengths of time.

The fact that small canid females occupy exclusive ranges and have restricted annual breeding seasons alone suggest that it may be difficult for males to regularly monopolise more than one fertile female (Emlen & Oring 1977). Added to this the requirement for a prolonged period of mate guarding, and it becomes even less likely that males could

routinely succeed in becoming polygynous. This implies that the canid pair bond (and thus social monogamy) could have evolved or be maintained largely or entirely because it increases male mating success. While studies of other mammal species have proposed that social monogamy may have evolved as a mate-guarding strategy (section 4.1.3), this idea has not previously been suggested to apply to Canids.

4.1.8 spatial organization and breeding synchrony in the bat-eared fox

Information on bat-eared fox spatial organization is limited, with only one study having tracked the movements of radio-collared animals (Malcolm 1986, but only for a single breeding season). The little data that is available suggests that the species may be less territorial than other canids: -

Lamprecht (1979), in a study conducted in the Serengeti, reported that minimal home range overlap between neighbouring pairs was the norm, and stated that interactions between neighbouring pairs tended to be aggressive. Malcolm (1986), by contrast, reported a high degree of home range overlap in the Masai Mara (with one of his 3 study groups having little area of exclusive use) and largely amicable relations between neighbours. This is in tune with observations from Southern Africa, where the species has repeatedly been described as being non-territorial, with neighbouring ranges overlapping widely, and little or no defence of ranges witnessed (Nel 1978, Mackie & Nel 1989, Lourens & Nel 1990).

Another potentially unusual feature of bat-eared fox social behaviour is that pairs may regularly disperse between breeding seasons. Lamprecht (1979) noted that the majority of pairs on his study site seemed to have disappeared by the next breeding season, and concluded that 'bat-eared foxes do not as a rule settle on the same breeding grounds year after year'. Maas (1993), however, reports that foxes on her Serengeti study site occupied stable territories over the course of 3 breeding seasons. It would be interesting and surprising if bat-eared foxes did disperse between breeding seasons, because breeding dispersal is rare in Canids (even in species occupying variable and harsh environments, e.g. Arctic fox, Strand *et al.* 2000), and mammalian monogamy is usually associated with long-term territoriality (Bradbury & Vehrencamp 1977).

While no previous studies have provided detailed information on the breeding synchrony within local populations, it is clear that bat-eared foxes are usually seasonal breeders, with cubs being born between late August and late October in East Africa (Lamprecht 1979, Malcolm 1986, Maas 1993), and between October and early December in Southern Africa (Pauw 2000, Nel *et al.* 1984). Birth peaks appear to be timed to coincide with periods of peak rainfall (and food availability, see Maas 1993).

The only previous description of bat-eared fox mating behaviour comes from a captive pair, which mated up to ten times a day for a week (Rosenburg 1971). Foxes were only observed mating once during the course of this study, with the pair remaining in a copulatory tie (with the male staying mounted) for at least five minutes.

4.1.9 Aims of chapter

This chapter has two primary objectives: -

The first of these is to present detailed data on bat-eared fox spatial organization (range sizes, range overlap of partners and neighbours, and range fidelity between breeding seasons) and breeding synchrony.

The second aim of the chapter is to investigate factors other than the requirement for male care that may favour the maintenance of social monogamy in the bat-eared fox. In this context, I attempt to answer the following questions: -

1) Are bat-eared foxes socially monogamous because males are incapable of defending sufficient resources to support more than one breeding female?

As was outlined in section 4.1.2, it has been proposed that monogamy may have evolved because males are rarely able to defend sufficient resources to support multiple females. We test this hypothesis by measuring variation in termite abundance on the territories of 10 males.

2) Given the degree of oestrous synchrony and spatial distribution of females on the study site, is it likely that males could routinely defend more than one fertile female?

As was discussed in section 4.1.4, the ability of males to defend multiple females is expected to vary according to the spatial and temporal distribution of fertile females, and the requirement for mate guarding. Given data on the temporal and spatial distribution of fertile females (presented in this chapter), and data on the period of courtship typical in the species (presented in chapter 5), I calculate the probability that males could defend multiple females throughout their fertile periods. I also investigate how levels of breeding synchrony effect the ability of paired males to seek extra-pair copulations.

3) To what extent to males and females compete for partners and territories?

As discussed in section 4.1.5, the costs and benefits of alternative reproductive strategies can be investigated indirectly through the observation of widowed animals. I investigate the degree to which males compete for partners, and therefore the likelyhood that any male could sequentially or simultaneously defend multiple fertile females, by observing how quickly widowed females re-pair.

4.2 Methodology

4.2.1 Calculation of home range size and overlap

All home ranges were calculated using 60 independent nocturnal radio-tracking fixes collected during the 20 weeks prior to parturition (using the protocol described in section 2.2). A maximum of 2 fixes were collected on any one night, and a minimum of 16 fixes were collected from each of the three (arbitrary) nocturnal time blocks (section 2.4).

Home ranges sizes (and overlap) were calculated using the Kernel technique, because this method provides the most accurate assessment of an animal's regular foraging range (see section 2.2.3). Having said this, analysis revealed that estimates of home range size and overlap did not differ according to whether this or the Minimum Convex Polygon (MCP) technique were used (For estimates of home range size: paired t-tests for all male data: $t=0.97$, d.f.=11, $p=0.35$. for all female data: $t=1.41$, d.f.=12, $p=0.19$. For estimates of home range overlap; paired t-tests for overlap of male ranges: $t=0.75$, d.f.=7, $p=0.48$, for overlap of female ranges: $t=0.05$, d.f.=7, $p=0.96$).

Before analysis of home range sizes was carried out the data were checked to ensure they met the requirements for parametric testing. Visual inspection of histograms revealed that fox home range sizes approximate a normal distribution. F-tests revealed that there were no significant differences in variances of home ranges between the sexes ($F=1.28$,

d.f.=11,12, p=0.33). Data were deemed suitable for parametric testing without transformation.

When presenting and analysing data on home range size, data collected from the same individuals (over more than one season) was treated as being independent. This was done because individual range sizes often varied markedly between seasons (section 4.3.3). Results generated were not qualitatively different from those produced if data from individuals were treated as being non-independent (range sizes for single foxes tracked over 2 years averaged to give a single value).

Home range overlap is presented for mated partners and neighbouring animals. Mated partners were easily identified because they were almost always found together (particularly during the day, see appendix 3.1), and no groups on the study site contained more than 2 adults. Neighbouring animals are defined as any non-paired adults with some degree of range overlap. Range overlap between dyads of animals is expressed as an area, and a % of each animals range (giving two values, one for each individual).

4.2.2 Estimation of dates of parturition and female oestrus

Parturition dates were most often inferred from regular checks of fox pairs during the birthing season. When females gave birth they typically spent 2/3 days inside a breeding den, and shortly after this cubs were often heard whimpering inside the dens. Prior to giving birth females typically rested above ground with their partners, sometimes but not

always close to the dens where they gave birth. After parturition females and their partners typically rested at or inside breeding dens. It was also possible to tell if a female has given birth on the basis of her size, heavily pregnant females being noticeably larger than non-pregnant females. In some cases parturition dates were estimates based on the size of cubs first seen (and using cubs of known age as points of comparison).

The degree of oestrous synchrony was estimated from the synchrony of parturition dates (which makes the assumption that females had equal gestation lengths).

4.2.3 Calculating whether male ranges contained sufficient food to support additional adults

We proposed that for a territory to contain sufficient resources to support an additional breeding female, it would have to contain 1.83 times the minimum termite abundance required for successful breeding. This figure is equal to the proportional increase in the maximum number of adult sized foxes the territory would have to hold; i.e. 11 animals (one male, 2 females and 8 cubs) versus 6 animals (one mated pair and 4 cubs)- see Brotheron & Manser 1997, who employ a similar calculation.

Total food abundance on male home ranges was calculated using the methods described in section 2.5.

4.2.4 Assessing the potential of males to monopolize multiple females

In order to assess the ability of males to monopolize females, I calculated how it would have been possible for males to engage in full courtship with two females, given the degree of oestrous synchrony observed in 2001.

I did this by firstly calculating differences in conception dates (in days) for all pair-wise combinations of 11 females on the study site (n=55). I then calculated, given different required periods of mate guarding, the proportion of these 110 combinations would have allowed a male to engage in full courtship with both females.

In a 2nd set of calculations, I assess the ability of males to seek extra-pair copulations. We do this by calculating the proportion of female-female combinations that provided males with the potential to guard their own mates and fertilize 2nd females (i.e. the 2nd females date of conception fell outside the male's mate-guarding period), again given different required lengths of mate guarding. This time, each pair-wise female-female combination contributed 2 values, one positive and one negative (thus n=110). This was done because any female conceiving *after* a given male's social partner was deemed to be available as a potential extra-pair partner, but only females conceiving *before* a male's mate guarding period were considered to be available as potential partners.

4.2.5 Observation of widowed foxes

I recorded the fate of 3 widowed females and 4 widowed males, noting if and how quickly animals re-paired, and whether or not they remained on their territories.

If competition for mates were more intense than competition for territories, we would expect individuals (of either sex) to disperse and search for new mates.
Conversely, if competition for territories were greater than competition for mates, we would expect individuals to remain on their territories and wait for any opportunity to re-pair (e.g. Morley & Balshine 2002).

4.3 Results

4.3.1 Home range sizes

Table 4.1 presents data on home range sizes of 15 foxes from 10 pairs. Average range sizes presented for males and females treat data collected from the same individuals (during different years) as being independent.

The average home range size of males was 3.31 km^2, but their range sizes varied considerably, from 0.88 km^2 to 9.14 km^2. Home range sizes for females were slightly smaller, averaging 2.88 km^2, and again they varied widely, from 0.59 km^2 to 8.45 km^2. The home ranges of males and females did not differ significantly in size, regardless of whether data from all individuals ($t=0.49$, d.f.=23, $p=0.62$) or data from mated partners was compared (paired t-tests- $t=1.73$, d.f.=7, $p=0.13$).

4.3.2 Patterns of home range overlap

Home range overlap of mated pairs

Table 4.2 presents data on the degree of home range overlap of 6 mated pairs collected in 2001 and 2002. Data is only presented for fox pairs in which partners were tracked concurrently (during the same year). Average values are presented per pair (with values from pairs tracked over 2 years averaged to give a single value).

Table 4.1 Home range sizes for 18 individual foxes (8 males and 10 females) from 10 social groups, calculated using the Kernel method. All range sizes are calculated from 60 independent radio-tracking fixes collected over a 6th month period prior to parturition.

Group	Year	Male ID	territory size (km^2)	Female ID	territory size (km^2)
Astra	2001	fm27	1.96	ff28	2.05
	2002	fm27	2.13	ff28	2.05
Junction	2001	-	-	ff29	3.89
	2002	fm22	4.08	ff29	3.50
Mzee	2001	fm23	6.18	-	-
Reflector	2000	-	-	ff8	2.79
Puffadder	2001	fm17	2.52	-	-
	2002	-	-	ff47	0.59
Snorer	2001	fm25	2.16	ff16	1.79
	2002	fm25	0.88	ff16	1.00
Ghost	2001	fm9	1.69	-	-
	2002	fm9	2.35	ff46	2.44
Everest	2000	-	-	ff19	4.50
	2001	fm20	3.61	-	-
	2002	fm20	9.14	ff62	8.45
Camp	2001	-	-	ff30	1.73
What	2002	fm54	2.77	ff55	2.64
		Males		Females	
	Mean	n	12	n	13
		$\bar{x}$	3.31	$\bar{x}$	2.88
		s.d.	2.27	s.d.	2.00

Table 4.2 Data on % home range overlap for all 'mated pairs' of foxes on the study site in 2001 and 2002. Home range overlaps are presented as an area (km^2) and as % of each animals territory.

		ID		Overlap		
Pair	Year	Male	Female	Area	% male	% female
Astra	2001	fm27	ff28	1.71	87.6	83.7
	2002	fm27	ff28	1.95	91.4	95.1
Snorer	2001	fm25	ff16	1.63	75.4	91.0
	2002	fm25	ff16	0.92	91.5	92.9
Ghost	2002	fm9	ff46	2.22	94.5	91.1
What	2002	fm54	ff55	2.19	78.8	83.0
Junction	2002	fm22	ff29	3.03	74.3	86.6
Everest	2002	fm20	ff62	8.04	88.0	95.1
Mean (per pair)			$\bar{x}$	3.10	84.8	89.5
n=6			s.d.	2.49	7.41	4.26

The data presented in Table 4.2 shows that the home ranges of mated partners overlap considerably. The average home range overlap of males with their partners was 84.8% (range 74.3-94.5). The % home range overlap for females was slightly higher, averaging 89.5% (range 83.0-95.1). Differences in % range overlap between the sexes are a consequence of the fact that male ranges were slightly larger than those of females (with the result that areas of overlap were necessarily a lesser proportion of the total range size). However, males and females did not differ in the degree to which their territories overlapped with those of their partners ($t=2.02$, d.f.=5, $p=0.10$).

Range overlap between neighbouring pairs

Table 4.3 presents data on the overlap of home ranges of 10 individual foxes from 8 pairs in 2001 (giving a total of 16 'dyads' of neighbouring individuals with some degree of home range overlap). Figures 3.1 shows Kernel home range plots for the same foxes.

It is immediately apparent from Figure 4.1 that the ranges of neighbouring foxes often overlap considerably. The average range overlap for all pair-wise combinations of neighbouring animals (n=32, with 2 values of range overlap for each of the 16 pair-wise combinations) was 22.7 %, but this varied largely between different neighbours. Of particular note, almost 50 % of the range of male fm25 overlapped with the range of neighbouring male fm20. Similarly, the range of male fm9 overlapped with both members of Astra pair (fm27 & ff28) by approximately 30%, and the range of male fm17 overlapped with both members of Astra pair (fm27 & ff28) by approximately 30%.

Table 4.3 Data on % home range overlap of Kernel ranges for all neighbouring foxes on the study site in 2001. Home range overlaps are presented as an area (km^2) and as % of each animals home range. The table also gives the mean (and s.d.) in % overlap for all neighbouring ranges, for male neighbours, for male-female neighbours and for female neighbours.

Animal A		Animal B		Overlap		
ID	Group	ID	Group	Area	% A	% B
fm20	Everest	ff 30	Camp	0.42	13.1	27.2
fm20	Everest	ff16	Snorer	0.92	23.1	51.3
fm20	Everest	fm25	Snorer	1.04	26.2	48.1
fm20	Everest	fm17	Puffadder	0.32	8.0	12.5
fm25	Snorer	ff29	Junction	0.40	18.5	10.3
fm25	Snorer	fm17	Puffadder	0.72	33.3	28.5
ff16	Snorer	fm17	Puffadder	0.55	30.5	31.7
ff16	Snorer	ff29	Junction	0.19	10.6	4.9
fm17	Puffadder	ff29	Junction	0.67	26.3	17.2
ff29	Junction	fm23	Mzee	1.16	29.7	19.1
ff29	Junction	fm27	Astra	0.43	10.9	21.8
ff29	Junction	ff28	Astra	0.57	14.7	28.0
ff28	Astra	fm23	Mzee	0.42	20.4	6.9
ff28	Astra	fm9	Ghost	0.60	29.6	35.7
fm27	Astra	fm9	Ghost	0.62	31.5	36.4
fm27	Astra	fm23	Mzee	0.38	19.5	6.3

mean overlap	n	$\bar{x}$	s.d.
all individuals	32	22.7	2.0
male-male	10	24.1	4.06
male-female	18	23.0	2.48
female-female	4	15.5	5.50

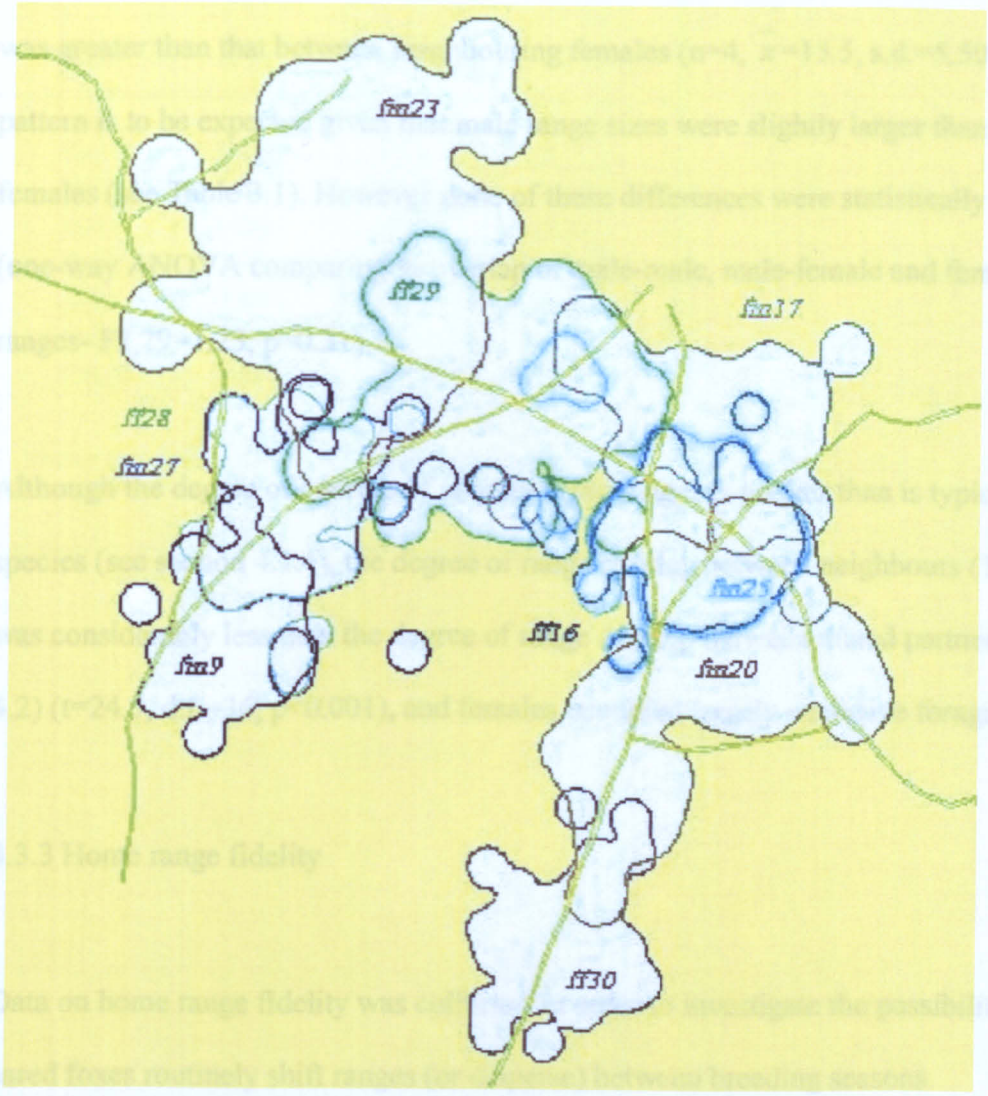

Figure 4.2 Kernel home ranges for 10 foxes tracked in the run-up to the 2001 breeding season. All ranges are calculated from 60 independent radio-tracking fixes.

The average % overlap between neighbouring males (n=10, $\bar{x}$=24.1, s.d.=4.06) was greater than that between males and females (n=18, $\bar{x}$=23.0, s.d.=2.48), which in turn was greater than that between neighbouring females (n=4, $\bar{x}$=15.5, s.d.=5.50). This pattern is to be expected given that male range sizes were slightly larger than those of females (see Table 3.1). However none of these differences were statistically significant (one-way ANOVA comparing % overlap of male-male, male-female and female-female ranges- $F_{2,29}$=1.23, p=0.31).

Although the degree of overlap of neighbouring ranges is greater than is typical of Canid species (see section 4.1.4), the degree of range overlap between neighbours (Table 4.3) was considerably less than the degree of range overlap between mated partners (Table 4.2) (t=24.5, d.f.=36, p<0.001), and females occupied largely exclusive foraging ranges.

4.3.3 Home range fidelity

Data on home range fidelity was collected in order to investigate the possibility that bat-eared foxes routinely shift ranges (or disperse) between breeding seasons.
Table 4.4 presents data on the degree of home range fidelity of 7 individual foxes.

Home range fidelity is expressed in terms of percentage of home range overlap between seasons. Mean values are presented and per pair (with data from the 2 sets of paired animals (fm27 & fm28, fm25 & ff16) averaged to give a single value).

Table 4.4 Home range fidelity, as measured by % of overlap of 7 individual fox home ranges between the 2001 and 2002 seasons.

		Range overlap	
Animal ID	area	% '01 range	% '02 range
fm27	1.46	59.4	80.3
ff28	1.44	58.7	83.6
fm9	1.06	63.7	45.8
fm25	0.90	41.8	89.2
ff16	0.84	46.7	83.9
fm22	3.07	78.9	97.7
fm20	3.61	95.0	35.5
mean per pair	$\bar{x}$	68.2	69.5
(n=5)	s.d.	19.4	27.2

Data presented in Table 4.4 shows that there is some degree of variability in the extent to which individual ranges overlap between years. 2001 ranges overlapped with 2002 ranges by an average of 63.5%, while 2002 ranges overlapped with 2001 ranges by an average of 73%. This was a consequence of the fact that 2002 ranges tended to be slightly smaller than 2001 ranges (hence the area of overlap was necessarily a greater % of the total range).

Although these data are limited, they do suggest a number of things about inter-seasonal variation in home range configuration. Generally speaking, bat-eared fox home ranges were fairly stable between seasons. No fox groups breeding on the study site shifted area completely, and long distance dispersal was only observed in young animals and males that had lost their partners (see section 4.3.6). That said, the data shows that fox home ranges are not entirely fixed entities, but can expand, contract and drift slightly between seasons. For example: -

The home range of the Everest group (male fm20) doubled in size between 2001 and 2002. This happened after the group expanded their range into the neighbouring territory vacated by the Camp group, following the death of the Camp female (ff30) and presumed dispersal of her partner. The group Everest pair thus went on to occupy what had previously been 2 territories.

By contrast, the home ranges of the Snorer foxes (fm25 & ff16) halved in size between 2001 and 2002. Although there was a trend for home range sizes to reduce between the

2001 and 2002 seasons, no other ranges reduced as drastically as those of the Snorer pair. It is interesting to note that it occurred at the same time that the neighbouring (Everest) group expanded their range (see above), resulting in the Everest range being approximately 10 times the size of that of the neighbouring Snorers.

A case of slight range drift occurred in the Ghost group (fm9), where the % Kernel range overlap between the 2 seasons was 63.7 and 45.8 % respectively. This shows that although the foxes home range increased slightly in size between the 2 seasons, it also must have shifted (as if the range simply expanded or contracted we would expect either the first or second overlap value to remain closer to 100%). It is not clear what prompted this slight range shift.

4.3.4. Breeding synchrony

Birth dates for all litters born to 13 groups of foxes on the study site are presented in Table 4.5. Interestingly, the pattern of breeding synchrony altered markedly during the course of the study. This is illustrated in Figure 4.4.

Up to March 2001, breeding on the study site was less synchronous than thereafter. Three pairs of foxes (Junction, Reflector and Everest) gave birth between December 2000 and February 2001 with two of these three groups (Junction and reflector) known to have given birth at a similar time the previous year. By contrast four pairs (Snorer, Puffadder, Ghost & Astra) gave birth in August and September of 2000. Hence the population

Table 4.5 Dates of all breeding attempts by fox groups on the study site between January 2000-September 2002. (Nr= pair not resident on study site at the time).

Group	Year	Date	Year	Date	Year	Date
Astra	2000	1-Sep	2001	12-Sep	2002	2-Sep
Ghost	2000	15-Aug	2001	18-Aug	2002	15-Aug
What	2000	unknown	2001	18-Sep	2002	24-Aug
Reflector	2000	1-Feb	2001	1-Feb	2002	Nr
Junction	2000	15-Jan	2001	20-Sep	2002	10-Sep
		6-Dec	-	-	-	-
Grebe	2000	Nr	2001	1-Sep	2002	Nr
Neils	2000	Nr	2001	22-Aug	2002	Nr
Mzee	2000	unknown	2001	15-Sep	2002	unknown
Snorer	2000	15-Aug	2001	1-Sep	2002	15-Aug
Everest	2000	unknown	2001	5-Feb	2002	unknown
		-	-	16-Sep	-	-
Puffadder	2000	15-Aug	2001	1-Sep	2002	unknown
Camp	2000	20-Sep	2001	8-Sep	2002	Nr
Hartebeest	2000	Nr	2001	Nr	2002	20-Sep

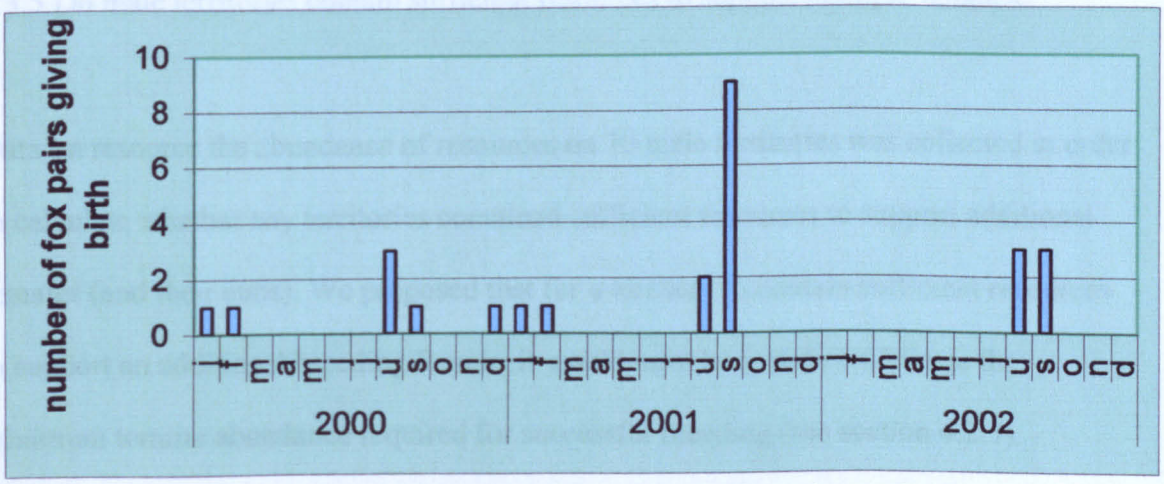

Figure 4.2 Number of fox pairs known to have given birth on the study site during each month of 2000, 2001 & 2002.

seemed to have two yearly birthing periods, one between December and February, and the other during August and September.

After March 2001, breeding on the study site became synchronized, with all 11 known groups of foxes on the study site giving birth during a five-week period between 18th August and 20th September. During this birthing peak, the average between-female difference in birth date (for all possible combinations of females) was only 12.6 days (n=55, S.D.=8.52). There was no significant difference in the degree of reproductive synchrony between females with neighbouring home ranges and those with no common borders (t=-0.41, d.f.=53, p=0.68).

Similarly, during 2002, all 6 known birth dates were between 15th August and 20th September.

4.3.5 Do male territories contain sufficient resources to support multiple females?

Data on resource the abundance of resources on 10 male territories was collected in order to calculate whether any territories contained sufficient resources to support additional females (and their cubs). We proposed that for a territory to contain sufficient resources to support an additional breeding female, it would have to contain 1.83 times the minimum termite abundance required for successful breeding (see section 4.2.3).

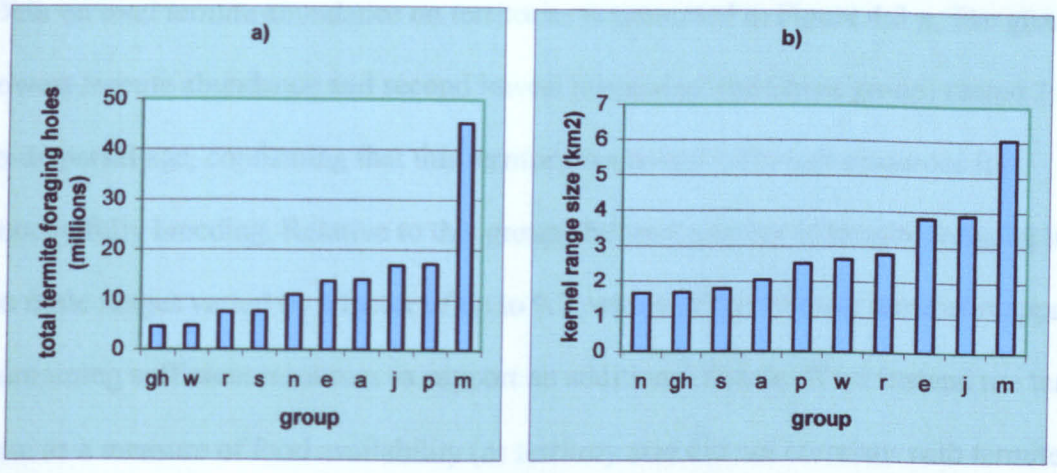

Figure 4.3 Variation in a) total termite abundance, and b) home range size across 10 male ranges during 2001

Data on total termite abundance on territories is presented in Figure 4.3 a. The group with lowest termite abundance and second lowest range size (the Ghost group) reared 2 cubs to dispersal age, confirming that this territory contained sufficient resources for successfully breeding. Relative to this group, the total number of termite foraging holes on male ranges varied by a factor of up to 9.7, with 6 of the 10 male territories apparently containing sufficient resources to support an additional female. If we instead use territory size as a measure of food availability (as territory size did not correlate with termite density; $r=0.25$, d.f.=8, N.S), 3 of the 10 territories contained sufficient resources to support and additional breeding female (Figure 4.3 b).

The data thus do not support the hypothesis that male territories never contain sufficient resources to support additional breeding females. The question of why foxes may occupy what appear to be unnecessarily large territories is addressed later (p 121).

4.3.6 Does female spatial and temporal distribution prevent males from monopolizing multiple oestrous females?

It is possible that males are incapable of becoming polygynous because female spatial and temporal distribution, combined with the requirement for a prolonged period of mate-guarding, make it unfeasible for males to monopolize more than 1 fertile female.

Data presented in section 4.3.2 show that, although the home ranges of female bat-eared foxes overlap partially, female spatial distribution effectively prevents males from

simultaneously maintaining proximity with more than one female. Males attempting to monopolise multiple females would therefore have to search for, court and mate with females sequentially. Figure 4.4.a illustrates the potential for males to sequentially guard multiple females according to different required lengths of mate guarding, given the degree of oestrous synchrony observed in 2001. I chose to perform these calculations on data from a synchronized breeding season (and not data from 2000) because seasonal breeding was observed during 2 of the 3 study seasons and is apparently the norm in other bat-eared fox populations (see section 4.1.5).

Not surprisingly, as the required period of mate-guarding increases, males become less capable of defending more than one female. If, in order to gain all or most paternity in a litter, males are required to guard females throughout their oestrous periods (of 7 days), then a majority (74.5% of) female-female combinations provide potential for polygyny. If, however, males are required to remain close to females during pro-estrus, the situation changes markedly: -

Data presented in section 5.3.2 shows that during the mating season partners (from 4 pairs) maintained close proximity for a period of at least 3 weeks. If this period of consortship is required to ensure successful mating, then only 18 % of female-female combinations provide potential for males to become polygynous. If the required period of mate guarding is 4 weeks, the potential for polygyny drops even further, to 5.5%.

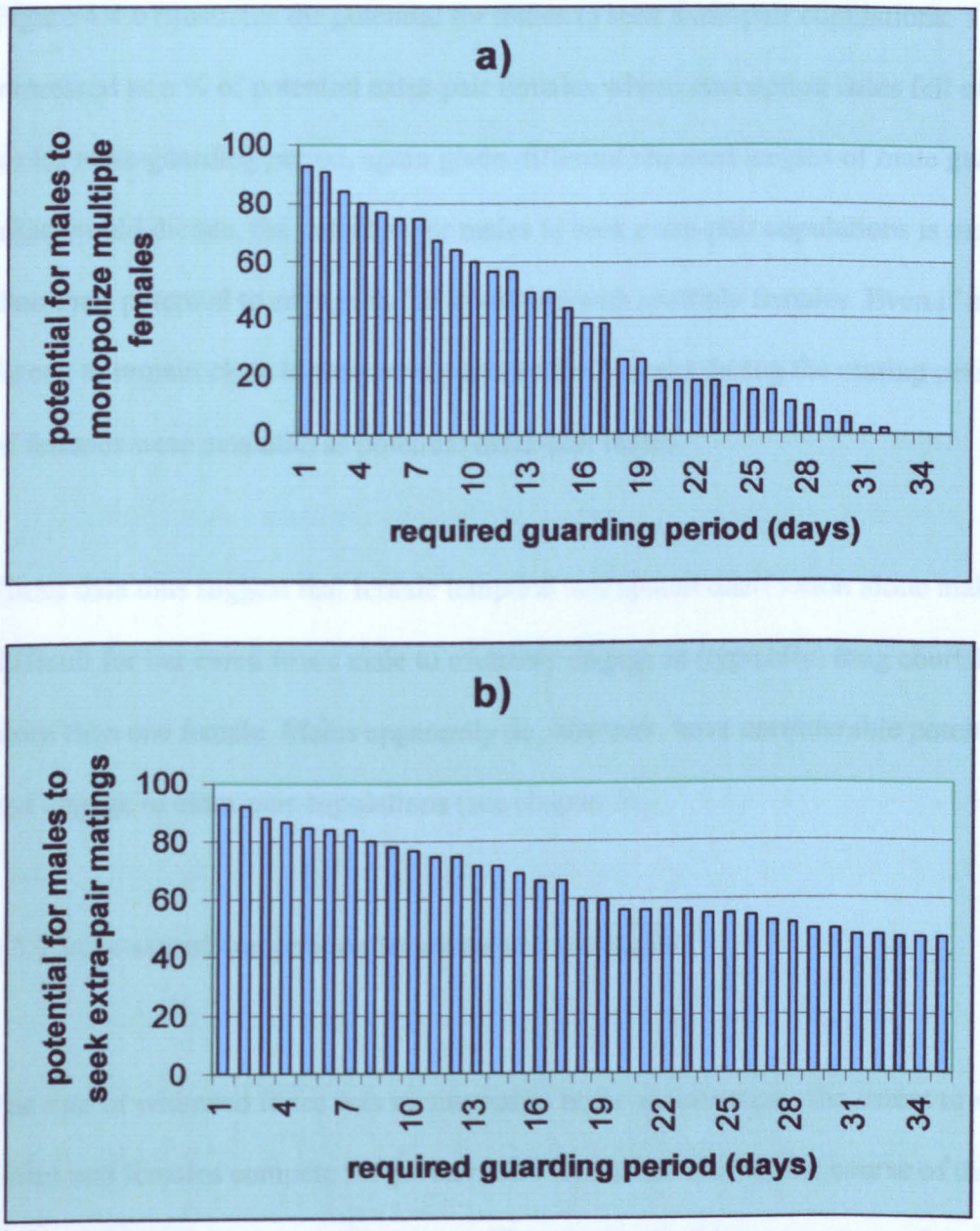

Figure 4.4 The ability of males to a) guard multiple females, and b) seek extra-pair copulations according to the required mate-guarding period.

Figure 4.4 b illustrates the potential for males to seek extra-pair copulations. This is expressed as a % of potential extra-pair females whose conception dates fell outside a males mate-guarding period, again given different required lengths of mate guarding. As logic would dictate, the potential for males to seek extra-pair copulations is much greater than their potential to engage in full courtship with multiple females. Even if males are forced to remain close to their own partners for 3 weeks during the mating period, 55 % of females were available as potential extra-pair mates.

These data thus suggest that female temporal and spatial distribution alone make it difficult for bat-eared foxes male to routinely engage in (typically) long courtship with more than one female. Males apparently do, however, have considerable potential to seek and engage in extra-pair copulations (see chapter 5).

4.3.7 Intra-sexual competition for mates and territories

The fate of widowed foxes was monitored in order to investigate the extent to which males and females compete for partners and territories. During the course of the project 4 males and 3 females lost their partners. The outcomes of these events are described in Table 4.6.

Table 4.6 shows that 2 of 3 widowed females retained their territories, and repaired within 2 weeks. In one of these cases the new male had previously been captured and seen resting on the periphery of his new partner's territory. In both cases the new male

showed no aggression towards the females large cub(s). The fate of the 3rd widowed female was less clear, but the fact that she was seen on her territory 4 weeks after her partners death, with her fully grown cubs (and possibly a new partner) confirms that she did not disperse immediately.

By contrast, the majority of males that lost partners appeared to disperse (two were assumed to do so, and one was later found dead approximately 15 km from it's territory). Only one of 4 males managed to repair and retain it's territory, but only after 6 weeks of extra-territorial prospecting.

Although limited, these observations suggest that there is intense inter-male competition for breeding vacancies, with partners apparently being in shorter supply than territories. The fact that females re-paired so quickly suggests that a population of 'floating' males exist, ready to rapidly fill any breeding vacancies that arise. This is further supported by the fact that one female re-paired with a male repeatedly seen resting on the border of her range. For females, on the other hand, territories may be in shorter supply than partners, although the ready supply of unpaired males means that widows rarely have to choose between the two.

Table 4.6 The outcome of 7 instances in which foxes lost their partners.

Case	sex of surviving partner	widowed animal radio-collared?	Outcome
1	female	yes	Female re-pairs within 10 days, without leaving territory. New male shows no aggression towards 4 month old cub.
2	female	yes	Female re-pairs within 14 days, without leaving territory. New male shows no aggression towards 4 five month old cubs.
3	female	no	Re-pairing rate not known, but female (and large cubs) sighted on territory 4 weeks after partners death.
4	male	yes	Male re-pairs 6 weeks after death of partner, following extended extra-territorial forays. Repeatedly found on range of neighbouring pair, associating with full sized female cub, before leading this female back to his original territory.
5	male	yes	Last found on territory 10 days after death of partner. 2 months later found dead 15 km from original territory, confirming long distance dispersal.
6	male	no	Male not sighted on territory again. Neighbouring pair expands range onto territory. Dispersal suspected.
7	male	no	Male not sighted on territory again. Two neighbouring pairs expand ranges onto territory. Dispersal suspected.

4.4. Discussion

4.4.1. Home range size and stability

Average bat-eared fox home range sizes reported in this study were 3.31 km^2 for males and 2.88 km^2 for females. Although male range sizes were slightly larger than those of females these differences were not significant. Home range sizes are similar to those reported by Malcolm (1986) in the Masai Mara, where 3 fox ranges of 3 radio-collared foxes averaged 3.53 km^2 (rounded minimum polygons calculated from 19, 41 an 66 fixes collected over 19, 15 an 19 week periods respectively).

Maas (1993) reports much smaller home range sizes on her Serengeti study site. Although she did not provide information on how she identified territory boundaries, scaled diagrams of 6 fox territories (Maas 1993- appendix 7) suggest that home ranges sizes varied between 0.5 and 1.0 km^2. Limited data presented by Lamprecht (1979) again suggests smaller home range sizes in the Serengeti of between 0.25 and 1.57 km^2 (for 9 ranges).

It is possible that reported variation in bat-eared fox home range sizes is related to diet. Throughout most of their range (Malcolm 1986), and on the study sites of Lamprecht (1979) and Maas (1993), foxes feed predominantly on the large harvester termite *Hodotemes mossambicus*. This termite is not found on Malcolm's Masai Mara study site or on my Laikipia study site, where foxes fed predominantly on *Odontotermes* and

Macrotermes termites respectively. While data from other study sites would be required to confirm this possibility, numerous other Canids studies of have shown that ranging patterns can vary widely according to the distribution of available food (e.g. red foxes, Macdonald 1983; Kit foxes, White & Ralls 1993; Arctic foxes, Stand *et al.* 2000).

Bat-eared fox home ranges were relatively stable over time. Although ranges did contract, expand and drift slightly between breeding seasons (section 3.3.3), breeding dispersal only occurred in males that had lost their social partners. These data demonstrate that bat-eared foxes on the study site do not routinely disperse and establish new territories between breeding seasons (which Lamprecht (1979) has suggested may occur in the Serengeti).

4.4.2. Range overlap of mated pairs.

The extent of home range overlap between mated pairs was high. Male ranges overlapped those of their partners by 84.8 %, while female ranges overlapped those of their partners by and 89.5 %. These values are generally higher than those reported for other species of fox. For example: -

The average range overlap between mated kit fox (*Vulpes macrotis*) partners has been reported to be 70% (White & Ralls 1993, for MCP home ranges) and 75% (Zoellick & Smith 1992, using the grid cell method). Geffen & Macdonald (1992) report degrees on range overlap between Blanford's fox (*Vulpes cana*) partners of 77.9 % (using 80%

minimum polygons). Overlap between Arctic fox family members is even smaller, being only 37.5% (of MCP ranges, Stand *et al.* 2000), though this study did not differentiate between the range overlap of mated pairs and related subordinates.

One species with a similar degree of range overlap between mated pairs is the crab-eating fox (*Cerdocyon thus*, Macdonald & Courtenay 1996), in which the ranges of mated pairs were found to overlap by an average of 85.1% (for restricted convex polygon ranges-). The high degree of range overlap in the crab-eating and bat-eared foxes probably reflects the high degree of behavioural synchrony between partners (in both species partners often forage together- Macdonald & Courtenay 1996, chapter 4).

4.4.3 Range overlap between neighbouring pairs

Degrees of home range overlap between neighbouring foxes were high, averaging 22.7%. Variation in home range overlap between neighbours was also high, with the ranges of some neighbours overlapping much more than others (to of maximum of 51.3%). Average home range overlap was greatest between neighbouring males (24.1%), intermediate between opposite sex adults (23%), and smallest between neighbouring females (15.5%). This was a consequence of the fact that female ranges, on average, being slightly smaller than male ranges.

Similar patterns of range overlap have been reported in other studies of bat-eared foxes. Malcolm (1986), who radio-tracked 3 groups of foxes in the Masai Mara, reported that

home ranges overlapped extensively, with one of his three groups having little or no area of exclusive use. In contrast Lamprecht (1979), who followed 9 groups of foxes in the Serengeti, suggested that as a rule home range overlap was minimal. He did however report that 2 of his groups had a range overlap of more than 60%. Overall, data from this study, that of Malcolm (1986), and reports by Koop & Velimirov (1982) and Nel & Bester (1983), combine to suggest that large degrees of range overlap between neighbouring pairs are a consistent feature of bat-eared fox sociality.

This large degree of home range overlap is apparently unusual among the canids (see section 4.1.4), and may be related to the bat-eared foxes uniquely insectivorous diet. Waser (1981) developed a mathematical model showing that the benefits of exclusive territory defence diminish as the renewal rate of a food source increases, and provided empirical data showing that the renewal rate of insect prey is high. Because bat-eared foxes forage on the surface for prey with an underground refuge, there presence is likely to have minimal impact on termite numbers, and prey renewal rates are likely to be very high (even relative to other types of insect prey). Consequently the costs of maintaining exclusive territories are likely to outweigh any potential benefits. In agreement with this bat-eared foxes, unlike some other species of canid, do not routinely patrol or urine mark territory boundaries (personal observation).

An alternative explanation for the high degree of overlap of neighbouring ranges is that they are a consequence of an increase in home range size during the mating season,

resulting from attempts by males and/or females to engage with 'extra-pair' mates. This possibility is investigated in chapter 5.

4.4.4. Reproductive synchrony

Data presented on reproductive synchrony presented in section 3.3.5 show an interesting pattern. Up to August and September of 2001, reproduction on the study site was asynchronous, with one seasonal birth peak between December and February, and a second in August and September. From August 2001 onwards reproduction became synchronised, with all foxes on the study site giving birth in August and September of 2001 and 2002.

Given that the minimum observed inter-birth interval between successful breeding attempts was about 11 months (for Junction group), the level of breeding synchrony observed in August/September 2001 would presumably not have come about if any of the 3 groups breeding at the beginning 2001 had successfully reared offspring. Similarly it is possible that if any of the pairs breeding in August/September 2000 had lost litters and held on to their territories (both the Grebe and Camp group males dispersed after their partners were killed during lacation), they may have attempted to breed in January or February of 2002.

In other words this data is consistent with a strategy whereby pairs breed annually when successful, but attempt to breed again after 6 months if reproduction fails in it's early

stages (this was observed in the Junction and Everest groups). More data is needed to confirm whether or not this is the case. An alternative possibility is that the asynchronous breeding reported at the beginning of the study was an aberration caused by the unusual weather conditions of 1998 and 1999 (1998 was an el nino year while 1999 was a drought year), and that one seasonal birth peak is the norm in this region.

4.4.5 which factors prevent bat-eared fox males from becoming polygynous?

Data presented in the previous chapter suggested that unrelated females should avoid becoming polygyny because there would be a cost to sharing (beneficial) male care. The situation for males though was less clear, and it is possible that males could increase their reproductive success by dividing their care between multiple litters. If this is the case, what is it that prevented males from becoming polygnous?

Distribution of resources on male territories

Murray (1984) and Gosling (1986) both suggested that monogamy may evolve or be maintained when males are incapable of defending territories large enough to support multiple breeding females. Data presented in section 4.3.4 suggest that this is not the case in bat-eared foxes. Whether we use total termite abundance or territory size as a measure of territory quality, some males occupied territories that were large enough to support an additional breeding female and her cubs. This is further suggested by the observation of

one pair expanding their range and going on to occupy what had previously been two territories (on which foxes had bred successfully, section 4.3.3).

These results suggest that the ability of males to defend resources sufficient to support multiple females does not necessarily correspond with an ability to defend multiple mates. There are a number of possible reasons why this may be the case (discussed later in this section). It also raises the issue of why some bat-eared fox pairs occupy territories that appear to be unnecessarily large. There are a number of possible answers to this question: -

Verner (1977) put forward the intriguing hypothesis that individuals may be selected to defend larger territories than they need for their own purposes simply out of spite, in order to prevent others in the population from using the resource. This hypothesis has been criticised, however, on the basis that the super-territory holder, while bearing the cost of increased territory defence, will also increase the relative success of other territorial individuals (Davies & Houston 1984).

Another possibility is that pairs adjust their territory size in order to ensure that their ranges contain sufficient food to support them during times of lowest food availability (see Macdonald 1983). If territories are defended as such long-term investments, then in some short-term periods they may appear to contain excess resources (Davies & Houston 1984). This hypothesis could explain the observed variation in territory quality, but only if fluctuations in resource abundance on different territories were temporally independent

(such that different territories on the study site simultaneously experienced good and bad conditions). Unfortunately I did not attempt to measure how territory quality varied over time.

An alternative explanation for this observation is that some pairs seek to defend a resource for their offspring to later inherit. This is consistent with (though not proven by) the fact young foxes may regularly establish territories next to (and sometimes overlapping) those of their parents (see Appendix 4.1, Maas 1993, Macdonald & Courtenay 1996), in areas where unrelated animals were apparently unable to do so. More data are required to investigate this possibility.

Spatial and temporal distribution of oestrous females

As discussed in section 4.1.3, when females are widely dustributed in space, and their oestrous periods are highly synchronized, it can be difficult or impossible for even the most competitive males to defend multiple females (Emlen & Oring 1977). Although the degree of range overlap between neighbouring female bat-eared foxes is greater than is typical of most other Canid species, females occupy what are essentially exclusive ranges. Because of this, males attempting to guard two (or more) oestrous females would almost certainly have to do so sequentially (rather than simultaneously).

As was discussed in section 4.2, the nature of female oestrus is likely to favour a prolonged period of mate guarding in Canids. Data presented in chapter 5 supports this

prediction, showing that during the mating season partners (from 4 fox pairs) maintained very close proximity for a period of least 3 weeks. Figure 4.3.a shows that, with the degree of reproductive synchrony observed in 2001, it would have been very difficult for bat-eared foxes male to routinely engage in typically (3 weeks) long courtship with more than one fertile female.

While it is not certain that a 3 week guarding period is required to ensure all or most paternity in a litter, these data do suggest that oestrous synchrony, combined with a requirement for prolonged mate-guarding, place a significant constrain male mating options (as has been shown by Say *et al.* 2001, Gehrt & Fritzell 1999).

Intra-sexual competition for mates

The fact that widowed females repaired so quickly (in both known cases within 2 weeks- see Table 4.3.7) suggests that males compete intensely for access to mates. This is further suggested by the fact that the majority of widowed males abandoned their territories (Table 4.3.7), presumably in order to search for new partners.

Because of this intense competition for females, it is unlikely that aspiring polygynists would ever be able to secure 2nd mates. Relative to unpaired males, males who already had partners would be incapable of investing the same and energy into courting (and displacing competing males from) widowed or unpaired young females. If they did,

because unattended females repair so quickly, they would face the considerable risk of losing their original partners (and territories).

Data presented in the previous chapter suggest that, because of the cost of sharing beneficial male care, females should avoid being recruited into polygynous groups (section 3.4.5). Although widowed females apparently had little choice as to whom they repaired with (see also Brotherton & Manser 1997), it is likely that they can easily avoid pairing with males who already have partners. Even if paired males did compete to gain additional partners (which, according to the argument presented above, they probably should not do), it would be relatively easy for females to detect their paired status, if only because these males would be incapable of maintaining the almost continuous levels of close proximity typical of mated bat-eared fox partners (see Appendix 3.1 and chapter 5).

Combined affect on male mating options

It seems likely that, because females occupy largely exclusive ranges and can readily detect a males paired status, they are in a strong position to prevent polygyny. Add to this the intense intra-male competition for mates, the possible requirement for prolonged mate guarding and a high degree of oestrous synchrony among dispersed females, and it seems very unlikely that males could ever successfully defend multiple dispersed females. The cost of doing so (particularly the reduced ability to defend their 1st mate, but also the costs of increased energetic expenditure and predation risk) would always outweigh the benefits. This suggests that polygyny would only be an option for males if (compliant)

females closely coordinated their behaviour. This conclusion is consistent with Maas' (1993) observation that polygynous bat-eared fox groups only formed when daughters delayed dispersal, and went on to breed and share a communal den with their mothers.

If males are incapable of defending multiple females, what is the best reproductive strategy they could adopt? Trivers (1972) has argued that males of socially monogamous species should adopt a 'mixed reproductive strategy', ensuring successful mating at home before seeking extra-pair copulations with other females. Macdonald (1992) has suggested that this behaviour may be commonplace among apparently monogamous male Canids. The question of whether or not bat-eared foxes do seek to mate outside the pair bond is addressed in the following 2 chapters.

4.4.6 Summary

There are theoretical reasons for believing that social monogamy is unlikely to have evolved in response to a requirement for male care (Dunbar 1995). Additionally, although male care enhances offspring survival in bat-eared foxes (chapter 3), it is possible that males could gain from polygyny. This chapter investigates factors other than the requirement for male care that might operate to prevent males from attaining polygynous status.

Mammalian monogamy has apparently most often evolved in the absence of a requirement for male care (Komers & Brotherton 1997), and several theories have been

proposed to explain why it may have done so. One theory proposes that social monogamy may evolve when females are asocial (dispersed in space), because males are never capable of defending territories large enough to support more than one female (Murray 1984). I found that this theory is unlikely to account for monogamy in bat-eared foxes, because at least some male territories appeared to contain sufficient resources to support additional breeding females.

Social monogamy may also evolve if females are asocial and their breeding is highly synchronized, because under these circumstances even the most competitive males may be unable to effectively monopolize more than one female. Data presented in this chapter suggest that the spatial and temporal distribution of fertile females place a major constraint on the mating options of male foxes: -

Although female ranges were found to overlap more than those of most other canids (probably as a consequence of their insectivorous diet) females occupy what are essentially exclusive ranges. As a result of this attempted polygynists would have to guard oestrous females sequentially (rather than simultaneously). Because of the degree to which females reproduction was synchronized, and the likely requirement for an extended period of mate guarding, it is very unlikely that males would routinely be able to do this. Added to this intense intra male competition (as demonstrated by the speed with which widowed females re-paired), and it seems extremely unlikely that even the most competitive males could successfully defend more than one (dispersed) female.

I conclude that polygyny could only be an option for males if females are willing to co-ordinate their behaviour to some degree. This conclusion is consistent with the observation of the circumstances under which polygyny does sometimes occur in the species (Maas 1993).

Chapter 5

Movement patterns and behaviour of foxes outside and during the mating season- do foxes seek to mate outside the pair bond?

5.1 Introduction

5.1.1 Social versus genetic monogamy

The advent of molecular techniques that accurately assign parentage has led to a revolution in our understanding of understanding of animal social behaviour, principally by revealing that social relationships are often very poor predictors of mating relationships (Hughes 1998). Nowhere is this better illustrated than in the case of monogamous birds.

It was originally assumed that social monogamy implied mating exclusivity, but it turns out that this is often not the case. Extra-pair copulations have been reported in over 115 species of socially monogamous bird (Ford 1983), and accumulating genetic evidence suggests that strict fidelity is likely to be the exception rather than the rule (Birkhead & Moller 1992). This supports Trivers' (1972) prediction that males of socially monogamous species should pursue a mixed reproductive strategy, providing care to the offspring of one female while attempting to obtain extra-pair paternity (EPP) by pursuing extra-pair copulations (EPC's).

Levels of extra-pair paternity (EPP) vary greatly between monogamous bird species (Petrie & Kempenaers 1998). In some species the majority of broods contain extra-pair young (e.g. the Reed Bunting, *Emberiza sheoniclus*, Dixon *et al.* 1994), while in others extra-pair young are absent or occur at very small frequencies (e.g. the Fulmar, *Fulmaris glaciaris*, Hunter *et al.* 1992). Levels of extra-pair paternity have been shown to vary between populations of the same species, and between years within the same populations (Petrie & Kempenaers 1998).

Extra-pair fertilizations were originally thought to reflect male self-interest (Trivers 1972), because it is easy to understand how males gain from attaining extra-pair paternity (they father more offspring). Consequently it was assumed that EPP resulted primarily from forced copulations or sneaky fertilization by satellite males. This assumption has been challenged by bird studies demonstrating that females often actively seek extra-pair copulations (Kempenaers, Verheyren & Dhont 1997; Currie *et al.* 1998, Double & Cockburn 2000), and there is now a growing acceptance that females often control extra-pair matings (Gowaty 1996).

There are a number of ways in which females can gain from mating with males other then their social partners (see Petrie & Kempenaers 1998 for review). Females may gain the direct benefits of access to the extra-pair males foraging range (Gray 1997), or his investment in her offspring (Nakamura 1998). Alternatively females may gain indirect (genetic) benefits from this behaviour. EPC's may guard against mate infertility (e.g.

Wetton & Parkin 1991), increase the variability of offspring (Birkhead & Moller 1992, Kampenaers *et al.* 1999) or avoid the deleterious effects of inbreeding (Sillero *et al.* 1996). Females may also seek to copulate with males whose genetic quality is superior to that of their partners. There is increasing evidence to suggest that this is often the main motive of female birds seeking extra-pair copulations (Hasselquist *et al.* 1996, Dunn & Cockburn 1999, Jennions & Petrie 2000).

Engaging in EPC's may also entail costs, and these may differ for males and females. If males can reliably predict the proportion of offspring they have sired, they may respond to female infidelity by reducing the amount of care they provide that females offspring (Trivers 1972; see chapter 3 for a fuller discussion of the relationship between paternity and paternal care). Females may also suffer increased harassment by their partners or extra-pair males (e.g. Brotherton *et al.* 1997) For both sexes engaging in EPC's may increase the risk of acquiring sexually transmitted diseases (Sheldon 1993), and for males extra-pair prospecting may trade-off with provisioning of their offspring (Westneat *et al.* 1990).

The opportunities for individuals to pursue extra-pair copulations are likely to be influenced by demographic factors. Decreasing density of breeding pairs, for example, may reduce the frequency of extra-pair paternity by increases the time it takes for individuals to find and assess extra-pair copulation partners (Gowaty & Bridges 1991). Increasing breeding synchrony may also reduce the ability of individuals to seek extra-pair copulations because it makes it progressively more difficult for males to

simultaneously guard their own partners (see below) and seek extra-pair mates (Saino *et al.* 1999, Thusius *et al.* 2001, but see also Scutchbury & Morton 1995).

5.1.2 Mate Guarding

Monogamous males exhibit a range of morphological and behavioural traits that minimize the likelihood of their partners being inseminated by other males (Parker 1970). The most obvious of these traits is mate guarding, in which males remain either in physical contact or close proximity to their partners during their fertile period. In mammals this behaviour is often referred to as consortship (e.g. Packer & Pusey 1983, Sherman 1989).

The benefit to mate guarding is that males are able to deter their partners from initiating and engaging in extra-pair copulations. The effectiveness of mate guarding has been tested in numerous bird species by the experimental removal of males during their partner's fertile periods. In all studies published to date, male removal resulted in increased extra-pair courtship and copulations attempts on the female (reviewed in Birkhead 1998). This demonstrates that mate guarding is effective in reducing levels of extra-pair paternity. However, the fact that EPP exists in species where males routinely guard their mates suggest that mate guarding is rarely 100% effective, apparently because it is often relatively easy for females to elude their mates (Johnsen *et al.* 1998, Kempenaers *et al.* 1995, Stutchbury & Neudorf 1998). .

Mate guarding entails costs to males as well as benefits. One of these is that guarding males are unable to simultaneously pursue extra-pair copulations (Westneat 1994). Other costs of mate guarding vary according to a species' ecology. In some species the maintenance of close proximity may severely decrease foraging efficiency (Komdeur 2001) and/or increase predation risk. In these situations it may pay males to adopt alternative paternity guards, such as frequent copulation (Birkhead & Moller 1992). By contrast in species in which males and females regularly maintain close association outside the breeding season, mate guarding may require little alteration of normal behaviour and thus carry little or no cost.

The benefits and expected duration of mate guarding in mammals are also predicted to vary according to the length of female oestrus, and according to whether ovulation is induced or spontaneous (Gomendio *et al.* 1998). The majority of canid species are spontaneous ovulators with relatively long oestrous periods. Canids typically mate repeatedly throughout an oestrous period of 7-10 days, suggesting that males are unable to pinpoint the precise timing of ovulation. Gomendio *et al.* (1998) predict that this situation should favour prolonged mate guarding.

5.1.3 Sexual fidelity in monogamous mammals

Relatively little is known about the mating behaviour of monogamous mammals, so it is not clear if monogamous mammals exhibit the range of genetic mating systems found in monogamous bird. There are at least 2 reasons why the mating behaviour of mammals

may differ from that of birds. Firstly the fact that mammals are terrestrial may place a greater time and energy constraint on the pursuit of extra-pair copulations, and/or make it more difficult for females to escape the attention of guarding partners. Secondly the fact that mammalian ova are ovulated simultaneously rather than sequentially (as happens in birds) means that females are fertile for very limited periods of time. This could make it more difficult for mammals to achieve extra-pair paternity, and reduce the benefit of seeking extra-pair copulations (Gomendio *et al.* 1998).

What is the evidence regarding sexual fidelity in monogamous mammals? EPC's have been observed in at least six monogamous species; these include three species of primate (*Callicebus moloch*, Mason 1966; *Hylobates syndactylus*, Palombit 1994 and *Hylobates lar*, Reichard 1995), two rodents (*Meriones unguiculatus*, Agren *et al.* 1989 and *Marmota marmota*, Goosens *et al.* 1998) and one carnivore (*Proteles cristatus*, Richardson 1986). One of these species, the aardwolf (*Proteles cristatus*), has a social system and ecology that are superficially similar to that of the bat-eared fox, being a socially monogamous termite-eating carnivore (although aardwolves are solitary foragers). During the mating season aardwolf territory boundaries seem to break down, and the most competitive males succeed in mating with several 'paired' females.

Assessments of monogamy based on genetic data have been performed on at least 13 species that are reportedly socially monogamous (reviewed in section 6.1.2). These studies demonstrate variation in levels of extra-pair paternity, but perhaps as a whole

suggest that strict mating fidelity is more common than in monogamous mammals than birds.

5.1.4 Do species of canid seek extra-pair copulation's?

Cuckoldry has been confirmed by genetic means in 3 species of canid. Two of these species, the African Wild dog and the Ethiopian wolf, are pack living species in which related subordinates assist a dominant breeding pair (see section 6.1.2). The island fox is the only small canid for which genetic paternity data are available. Roemer *et al.* found that 25 % (4 of 16) of offspring tested had been sired by males other than their social father. This corresponds with behavioural data showing that the home ranges of male island foxes are up to four times larger during the winter, when courtship and mating occur (Fausett 1982, cited from Zabel & Taggart 1989).

With the exception of the island fox, evidence on the mating behaviour of monogamous foxes relies mainly solely on information on the movement patterns of males and females during the mating season. In a number of species males roam widely during the mating season, apparently in pursuit of extra-pair mates: -

White and Harris (1992) report that, for a limited time during winter, male red foxes (*Vulpes vulpes*) trespass into neighbouring territories, and suggest that these males are likely to be seeking extra-group matings. This wayfaring behaviour increases male seasonal home range sizes by a factor of 2.5, and the overlap of ranges with those of

neighbours by a factor of 7.5 (Whit & Harris 1992). This behaviour has also been reported by Voigt & Macdonald (1984), who estimated that the alteration of male ranging behaviour (during the mating season) increases the probability of inter-group encounters by a factor of 10.

Two studies of Kit foxes (*Vulpes* macrotis) suggest that males of this species also expand their home ranges during the mating season in the pursuit of extra-pair copulations. White *et al.* (2000) report that '2 mated male kit-foxes trespassed into neighbouring territories during the breeding season, probably in search of extra-pair copulations'. Zoellick and Smith (1992) report that 'much of the (range) overlap of non-paired animals (Kit foxes) was because of movements of males during the breeding season to dens used by females of other pairs'.

By contrast Geffen & Macdonald (Geffen & Macdonald 1992) presented seasonal home range data for Blanfords foxes (*Vulpes cana*) collected over the 4 quarters of the year. They found no evidence that male or female foxes increased their home range sizes or travelling distances during the mating season (winter).

So behavioural evidence suggests that males of some species of fox actively seek extra-pair copulations, while in other species they may not. Ranging data provide no evidence to suggest that females expand their ranges in the search for extra-pair matings. Clearly more behavioural and genetic evidence is needed to tests Macdonald's (1992) assertion

that cuckoldry may be commonplace amongst apparently monogamous male canids once they have mated successfully at home.

5.1.5. Do male or female bat-eared foxes seek extra-pair copulations, and which factors promote or constrain this behaviour?

Data presented in chapter 4 show that although breeding is highly synchronised (section 4.4.5), there is at least some scope for males to attempt to seek extra-pair copulations before or after their partners fertile period (section 4.4.7). This chapter presents the first data on the ranging patterns and behaviour of bat-eared foxes during and outside of the mating season. These data address the following questions: -

1) *Do either males or females actively seek EPC's ?*

I assess whether or not male or female foxes seek extra-pair copulations by asking the following questions: -

a) Do the range sizes of male or female foxes increase during the mating season?

Radio-tracking data presented in chapter 3 showed that, in the 6 months leading up to parturition, the home ranges of neighbouring foxes often overlapped considerably. In this chapter I investigate the possibility that this large degree of range overlap was a consequence of an increase in range size during the mating period.

b) Do rates of interaction between neighbouring foxes increase during the mating season?

If bat-eared foxes do seek extra-pair copulations we might predict interactions between neighbouring groups to be more common in the run-up to the mating period than during gestation. Rates of interaction between dyads of neighbouring foxes are compared between the 10 weeks leading up to and including the mating season and the 10 week gestation period.

c) Do travelling distances of male or female foxes increase during the mating season?

If foxes actively search for extra-pair copulations we might predict an increase in travelling distances during the mating season. Travelling distances of foxes were obtained from the observation of habituated foxes, and comparisons made between the run-up to the season, during the mating season and during gestation.

2) *Which factors promote or constrain the ability of males and females to attain extra-pair matings?*

a) Do male foxes guard their mates?

The occurrence and nature of mate guarding was investigated by comparing the proximity of fox partners and the extent to which males and females were responsible for maintaining proximity before the mating period, during the mating period and during gestation. If male bat-eared foxes guard their mates we would predict either: -

i) an increase in partner proximity during the mating period, with males

becoming increasingly responsible for maintaining proximity, or

ii) high levels of proximity across time periods, with males always more responsible for maintaining proximity.

b) Is mate guarding energetically costly?

If mate guarding carries a high energetic cost we would predict significant decreases in feeding rates during the mating season and possibly a reduction in feeding rate with increasing partner proximity. The energetic costs of mate guarding were investigated by comparing the time budgets of male and female foxes before, during and after the mating season, and by seeing if partner proximity affects feeding rate (during and outside of the mating season).

c) Do bat-eared foxes have time to seek extra-pair copulations?

The diet of a species affects that species time and energy budgets. In order to meet their energy requirements, insectivorous species like the Bat-eared fox may spend considerable amounts of time foraging. The more time a species spends foraging, the less time it will have available to engage in alternative activities, such as searching for extra-pair mates. I present data on bat-eared fox time budgets in order to investigate the energetic cost of extra-pair prospecting.

5.2. Methods

5.2.1 Analysis of male and female home range sizes during and outside the mating season

If bat-eared foxes seek extra-pair copulations, we might expect that the home range sizes of males and females to increase during the mating season. I investigated this possibility by comparing territory sizes at different stages in the breeding cycle during 2001. I made the following two comparisons: -

1) Firstly I compared MCP and Kernel home range sizes of males and females calculated from 30 radio-tracking fixes collected: -
   i) during the 10 weeks leading up to given pairs date of conception, versus;
   ii) during the females10 week gestation period.
2) Secondly I made a comparison between MCP and Kernel home range sizes of males and females calculated from 30 radio-tracking fixes collected: -
   i) during the 10 weeks closest to the main mating period on the study site, from 29th May to 7th August (5 weeks either side of 3rd July, when conception peaked).
   ii) during 10 weeks outside of the above period (but within the 20 weeks prior to parturition).

Female fertile periods were calculated by backdating 65 days (the approximate gestation length of the Bat-eared fox (Lamprecht 1979, Smithers 1983, personal observation)) from the date of parturition (see section 3.2.3).

If females seek extra-pair copulations we might predict that their range sizes will

be greater in the 10 week run-up to conception than during their 10 week gestation periods. If males seek extra-pair copulations we might predict an increase in male range sizes during the 10 weeks closest to the main mating period on the study site, and/or during their partners gestation period (if males seek extra-pair copulations only after mating successfully with their own partners).

5.2.2 Rates of interaction between mated partners and neighbouring foxes

The degree of interaction between both paired and neighbouring foxes was investigated by obtaining 'simultaneous' radio-tracking fixes from dyads of foxes. During 2001, we obtained 60 simultaneous radio-tracking fixes from 16 different dyads of neighbouring foxes. Additionally we obtained 60 simultaneous fixes from 3 different mated pairs. All fixes were obtained in the 20 weeks leading up to parturition.

Locations collected within 15 minutes of each other were considered to be 'simultaneous', as a smaller cut-off time would have made it difficult to collect sufficient data from neighbouring foxes. The degree of association in the movements of foxes (or dynamic interaction- Doncaster 1990) was investigated by comparing the observed separation distances of with an expected distribution of separation distances based on all possible distances measured from pair-wise recombinations of all the fixes (Doncaster 1990, analysis carried out using Wildtrak, Todd 1992). Chi-square tests were used to investigate observed separation distances deviated significantly from those expected by chance.

We compared levels of association between partners and neighbours: -

1) Across all 60 fixes collected in the 20 weeks leading up to parturition

2) For the first 30 fixes collected primarily in the 10 weeks leading up to mating

3) For the last 30 fixes collected primarily during females gestation periods

If foxes seek extra-pair copulations, we might predict that levels of association between neighbours would be greater than expected by chance in the run-up to the mating season, but probably not during the gestation period.

5.2.3 Mate guarding, travelling distances and time and energy budgets

Data on mate guarding, travelling distances and time and energy budgets were obtained through the direct observation of habituated fox pairs. During 2002, the behaviour of 3 pairs of habituated fox pairs (the 'Snorer', 'Astra' and 'Junction' pairs) were recorded during the run up to the mating season, during the mating season, and during gestation. The behaviour of a fourth pair (the 'What' pair) was recorded only during the mating and gestation periods). The mating season was defined, retrospectively (backdating from known parturition dates), as the period between 7th June and 7th July.

One animal from each pair was followed 3 times during each period, once during each nocturnal time block (see section 2.3.2). During each 'follow', a pair was observed 20 times at 10-minute intervals (or as close as possible). During each of the 20 observations we recorded: -

1) The behaviour of the fox(es) present, according to behavioural categories defined in section 2.3.3

2) The proximity of foxes to their partners. When both members of a pair were present, we estimated the distance between partners through observation. When only one member of a pair was present we estimated the distance to it's partner according to the strength of the signal from it's radio-collar to the nearest 100m- although there may have been a degree of inaccuracy in this technique it gave an idea of whether an animal was 'in the area', and allowed an rough estimate of partner proximity.

3) Location of foxes and distance travelled between successive observations. During each sighting, the location of the fox(es) was recorded using a hand-held GPS (Garmin 2). Travelling distances were calculated as straight-line distances between successive locations (clearly an underestimate given the typical meandering paths of forging foxes).

4) The degree to which each member of a pair was responsible for maintaining proximity with its partner. An individual was assigned as being responsible for maintaining proximity if: -

i) both animals were walking, and one animal was clearly following is partner,

ii) one or both animals were foraging, and one animal was clearly seen approaching to within 5m of its partner. If partners were not moving when first sighted, we waited and recorded which animal was first to perform one of the above behaviours.

5.3 Results

5.3.1 Proximity of fox partners before, during and after the mating season

Data on the proximity of mated fox partners were collected from 4 fox pairs before the mating season, during the mating season, and during the gestation period. The purpose of these data was to investigate how much time foxes spent close to their partners, and to see if levels of partner proximity increased during the mating season. These data are presented in Table 5.1 and Figure 5.1.

Figure 5.1 shows that the 4 fox pairs vary in the extent to which partners maintain proximity. 2 pairs (Junction and Astra groups) adjusted their behaviour with season, maintaing close proximity during the mating period, but frequently being found apart during the pre-mating and gestation periods. Statistical analysis reveals that partner proximity varied significantly with season for both of these pairs (Junction pair- X^2=85.4, d.f.=8, $p<0.01$; Astra pair- X^2=56.5, d.f.=8, $p<0.01$). By contrast 2 pairs (Snorer & What) did not appear to adjust their behaviour by season, but instead maintained similarly close proximity inside and outside of the mating period. Statistical analysis reveals no significant seasonal variation in partner proximity for these pairs (Snorer pair- X^2=10.8, d.f.=8, N.S.; What pair- X^2=6.85, d.f.=4, N.S.).

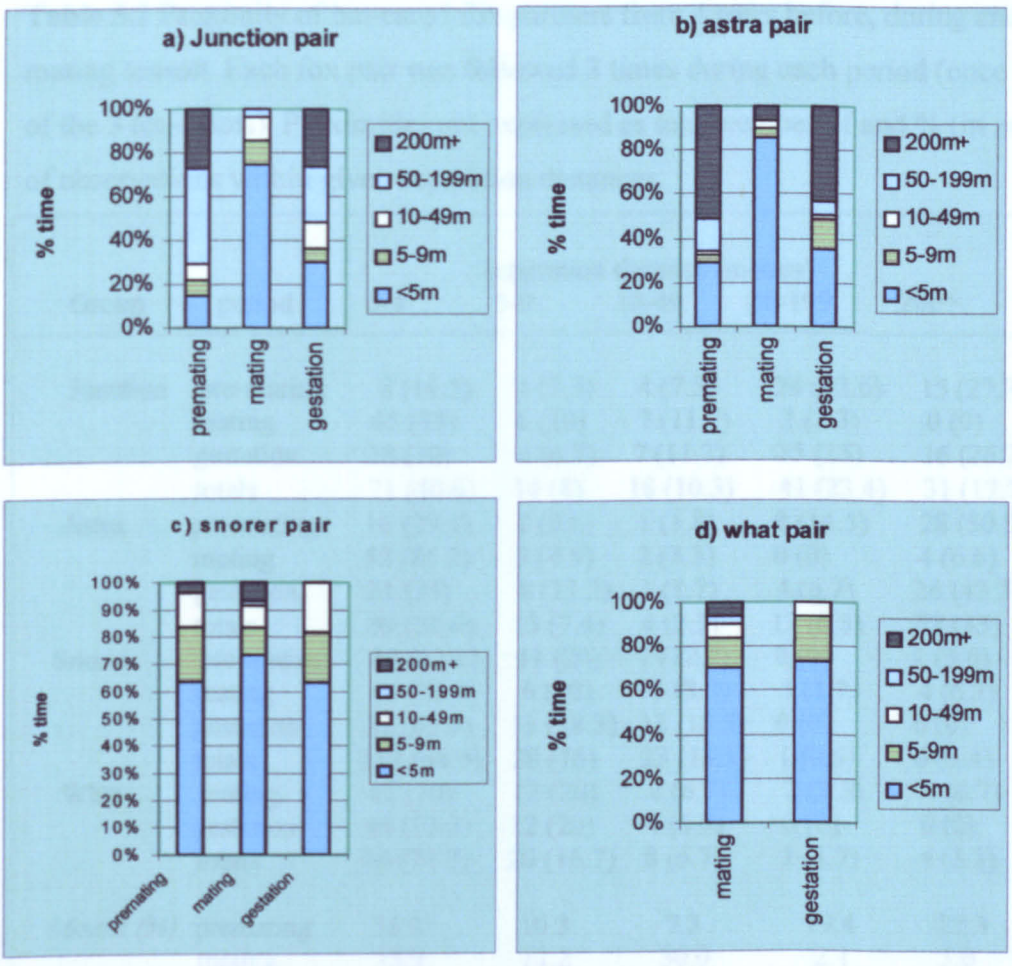

Figure 5.1. Proximity of bat-eared fox partners from 4 pairs before, during and after the mating season. Each fox pair was followed 3 times during each period (once during each of the 3 nocturnal time slots). Proximities are expressed as a % of observations within given distances of separation.

Table 5.1 Proximity of bat-eared fox partners from 4 pairs before, during and after the mating season. Each fox pair was followed 3 times during each period (once during each of the 3 time slots). Proximities are expressed as total number of and % (in parenthesis) of observations within given separation distances.

		Separation distance (metres)				
Group	period	0-4	5-9	10-49	50-199	200+
Junction	pre-mating	8 (14.5)	4 (7.3)	4 (7.3)	24 (43.6)	15 (27.3)
	mating	45 (75)	6 (10)	7 (11.7)	2 (3.3)	0 (0)
	gestation	18 (30)	4 (6.7)	7 (11.7)	15 (25)	16 (26.7)
	totals	71 (40.6)	14 (8)	18 (10.3)	41 (23.4)	31 (17.7)
Astra	pre-mating	16 (29.1)	2 (3.6)	1 (1.8)	8 (14.5)	28 (50.9)
	mating	52 (85.2)	3 (4.9)	2 (3.3)	0 (0)	4 (6.6)
	gestation	21 (35)	8 (13.3)	1 (1.7)	4 (6.7)	26 (43.3)
	totals	89 (50.6)	13 (7.4)	4 (2.3)	12 (6.8)	58 (33)
Snorer	pre-mating	35 (63.6)	11 (20)	7 (12.7)	0 (0)	2 (3.6)
	mating	44 (73.3)	6 (10)	5 (8.3)	1 (1.7)	4 (6.7)
	gestation	38 (63.3)	11 (18.3)	11 (18.3)	0 (0)	0 (0)
	totals	117 (66.9)	28 (16)	23 (13.1)	1 (0.6)	6 (3.4)
What	mating	42 (70)	12 (20)	4 (6.7)	2 (3.3)	4 (6.7)
	gestation	44 (73.3)	12 (20)	4 (6.7)	0 (0)	0 (0)
	totals	86 (71.7)	20 (16.7)	8 (6.7)	2 (1.7)	4 (3.3)
Means (%)	premating	35.7	10.3	7.3	19.4	27.3
	mating	75.9	11.2	30.0	2.1	5.0
	gestation	50.4	14.6	9.6	7.9	17.5
	totals	57.5	12.0	8.1	8.1	11.9

The overall effect of this was that there was little inter-pair variation in partner proximity during the mating period, when partners from all 4 pairs maintained close proximity (X^2=12.3, d.f.=12, N.S.). By contrast, there were significant inter-pair differences in proximity during both the pre-mating (X^2=82.5, d.f.=8, $p<0.01$) and gestation (X^2=108.5, d.f.=12, $p<0.01$) periods.

These data suggests that there is a degree of flexibility in the behavioural strategies of fox pairs on the study site.

5.3.2 Sex differences in the maintenance of pair proximity during and outside the mating season

Table 5.2 presents data showing how often male and females from each focal pair were seen following their partners during and outside of the mating season. This data is also presented graphically in Figure 5.2.

Visual inspection of Figure 5.2 suggests that there is considerable inter-pair variation in the extent to which each sex is responsible for maintaining proximity with its' partner, both during and outside the mating period. In the Junction pair the female spent far more time following its' partner than visa versa, while for the Snorer pair the opposite was true. The Astra and What pairs showed greater similarity between the sexes. The extent to which each sex was responsible for maintaining proximity varied significantly between pairs both during (X^2=20.6, d.f.=3, $p<0.01$) and outside the mating season (X^2=19.1, d.f.=3, $p<0.01$).

Table 5.2 Sex differences in maintenance of pair proximity for 4 fox pairs during and outside the mating season. The table shows the number of times that males and females of each pair were clearly seen following their partners during and outside of the mating period.

Group	Junction		Astra		Snorer		What	
Following	m	f	m	f	m	f	m	f
Mating	13	35	20	16	17	3	19	25
Non-mating	6	14	9	21	38	12	16	13
Totals	19	49	29	37	55	15	35	38

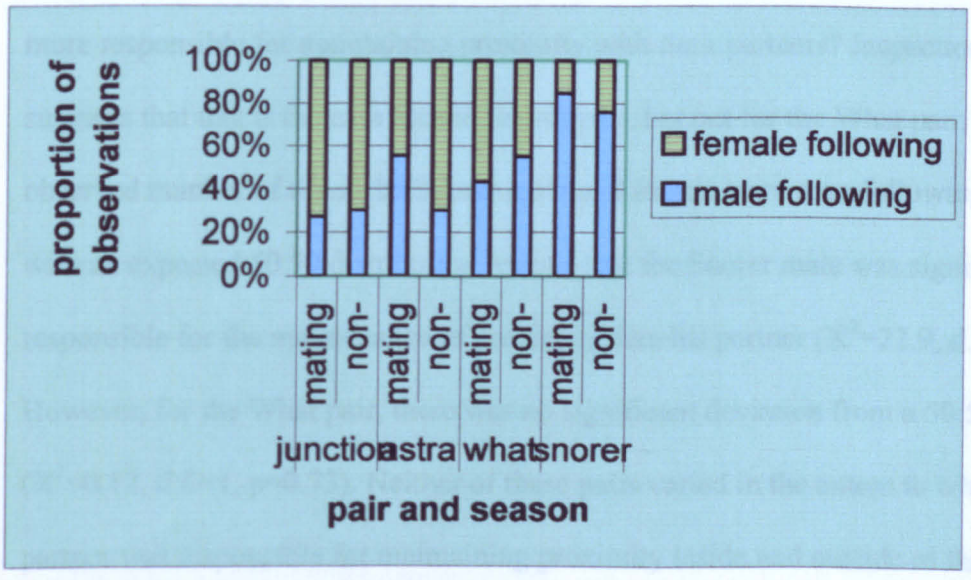

Figure 5.2 Proportion of time that males and females follow their partners (expressed as a % of all observations where one animals was clearly seen to be following the other) for the 4 focal fox pairs during and outside the mating season.

The Junction and Astra pairs spent significantly more time together during the mating season (see section 5.3.1). Were the males of these pairs responsible for this increase in proximity? Data suggest that for the Astra pair the answer is probably yes, as the male followed the female significantly more often during the mating season than he did outside this period (X^2=4.3, d.f.=1, $p<0.05$). However, there was no evidence that the junction male became increasingly responsible for maintaining proximity with its' partner during the mating season (X^2=1.27, d.f.=1, N.S.), in fact there was a slight increase in the proportion of time that his partner followed him (Figure 5.2).

The Snorer and What pairs showed now significant variation in partner proximity during and outside of the mating season (section 5.3.1). Were the males from these pairs always more responsible for maintaining proximity with their partners? Inspection of Figure 5.2 suggests that this is the case for the Snorer pair, but not for the What pair. Comparing the observed number of times the Snorer male and female were seen following each other with an expected 50:50 distribution reveals that the Snorer male was significantly more responsible for the maintenance of proximity than his partner (X^2=22.9, d.f.=1, $p<0.001$). However, for the What pair, there was no significant deviation from a 50:50 distribution (X^2=0.12, d.f.=1, $p=0.73$). Neither of these pairs varied in the extent to which each partner was responsible for maintaining proximity inside and outside of the mating season (for Snorer pair- X^2=0.69, d.f.=1, $p=0.69$; for What pair X^2=1.00, d.f.=1, N.S.).

The data therefore provides only limited support for the idea that males guard their mates. Although data from the Astra and Snorer pairs support the predictions of the male mate guarding hypothesis, data from the Junction and What pairs do not. This suggests that

benefits of maintaining close proximity with partners exist for females as well as males, both inside and outside the mating season.

5.3.3 Time budgets of foxes during the pre-mating, mating and gestation periods

Bat-eared fox time budgets were investigated to infer the amount the amount of 'free time' foxes have available to engage in non-essential activities, like the pursuit of extra-pair mates. Time budgets are also compared during and outside of the mating season to see if activities associated with mating, and in particular the close proximities foxes maintain with their partners, interferes with feeding.

Data on the time budgets of males and females from the 4 focal study pairs are shown in Tables 5.4 and 5.3 respectively. These tables give a breakdown of individual behaviour by season and the combined behaviour of individual animals across all seasons. Figure 5.3 provides a graphical illustration of the overall time budgets of the four focal pairs.

It is immediately apparent from Figure 5.3 that foxes are active for the vast majority of the night. The 6 foxes from the Junction, Astra and What pairs spent approximately 15 % (range 14.2-16.7%) of the night resting, while the male and female from the Snorer pair spent approximately 30 % (29.8 & 30.4% respectively) of the night resting. For the majority of the time foxes were travelling around their territories (range 8.6-19.3%), actively searching for food (range 11.3-24.8 %) and feeding (range 34.3-50.9%).

Table 5.3 Time budgets of female foxes before the mating period, during the mating period and during gestation. Each female was watched 3 times during period, once during each time slot. The table shows the number of observations and the % of time (in parenthesis) foxes were seen performing each activity.

			behaviour				
Group	ID	period	walk	search walk	feed	rest	other
Junction	ff29	pre-mating	2 (5.9)	5 (14.7)	7 (20.6)	17 (50)	3 (8.8)
		mating	2 (3.6)	19 (34.5)	29 (52.7)	0 (0)	5 (9.1)
		gestation	5 (17.9)	5 (17.9)	16 (57.1)	0 (0)	2 (7.1)
		totals	9 (7.7)	29 (24.8)	52 (44.4)	17 (14.5)	10 (8.5)
Astra	ff28	pre-mating	5 (9.6)	11 (21.2)	18 (34.6)	15 (28.8)	3 (5.8)
		mating	8 (14.3)	14 (25)	25 (44.6)	5 (8.9)	4 (7.1)
		gestation	18 (34)	12 (22.6)	15 (28.3)	5 (9.4)	3 (5.6)
		totals	31 (19.3)	37 (23)	58 (36)	25 (15.5)	10 (6.2)
Snorer	ff16	premate	4 (8.5)	7 (14.9)	21 (44.7)	12 (25.5)	3 (6.4)
		mate	1 (2.1)	6 (12.8)	13 (27.7)	22 (46.8)	5 (10.6)
		gestate	9 (16.6)	8 (14.8)	21 (38.9)	11 (20.4)	5 (9.3)
		totals	14 (9.5)	21 (14.2)	55 (37.2)	45 (30.4)	13 (8.8)
What	ff55	mating	6 (10.3)	15 (25.9)	26 (44.8)	7 (12.1)	4 (6.9)
		gestation	3 (5.6)	7 (13)	31 (57.4)	11 (20.4)	2 (3.7)
		totals	9 (8)	22 (19.6)	57 (50.9)	18 (16.7)	6 (5.4)
Means (%)		premating	8.0	16.9	33.3	34.8	7.0
		mating	7.6	24.6	42.5	17.0	8.5
		gestation	18.5	17.1	45.4	12.6	6.4
		totals	11.1	20.4	42.1	19.3	7.2

Table 5.4 Time budgets of male foxes before, during and after the gestation period. Each male was followed 3 times per period, once during each time slot. The table shows the number of observations and the % of time (in parenthesis) foxes were seen performing each activity.

			number and frequency of observation of behaviours				
Group	ID	period	walk	search	feed	rest	other
Junction	fm22	pre-mating	4 (9.8)	8 (19.5)	8 (19.5)	19 (46.3)	2 (4.9)
		mating	6 (10.7)	20 (35.7)	24 (42.9)	1 (1.8)	5 (8.9)
		gestation	7 (16.7)	6 (14.3)	25 (59.5)	0 (0)	4 (9.5)
		totals	17 (12.2)	34 (24.5)	57 (41)	20 (14.4)	11 (7.9)
Astra	fm27	pre-mating	4 (20)	3 (15)	5 (25)	6 (30)	2 (10)
		mating	6 (11.5)	14 (26.9)	23 (44.2)	5 (9.6)	4 (7.7)
		gestation	7 (25.9)	6 (22.2)	6 (22.2)	5 (18.5)	3 (11.1)
		totals	17 (17.2)	23 (23.2)	34 (34.3)	16 (16.2)	9 (9.1)
Snorer	fm25	pre-mating	3 (6)	7 (14)	24 (48)	12 (24)	4 (8)
		mating	1 (2)	5 (10)	17 (34)	22 (44)	5 (10)
		gestation	9 (16.6)	8 (14.8)	21 (38.9)	11 (20.4)	5 (9.3)
		totals	13 (8.6)	17 (11.3)	63 (41.7)	45 (29.8)	13 (8.6)
What	fm54	mating	7 (13.5)	15 (28.8)	21 (40.4)	6 (11.5)	3 (5.8)
		gestation	3 (5.6)	9 (16.7)	30 (55.6)	9 (16.7)	3 (5.6)
		totals	10 (9.4)	24 (22.6)	51 (48.1)	15 (14.2)	6 (5.7)
Means (%)		premating	11.9	16.2	30.8	33.4	7.6
		mating	9.4	25.4	40.4	16.8	8.1
		gestation	16.2	17.0	44.1	13.9	8.9
		totals	11.9	20.4	41.3	18.7	7.8

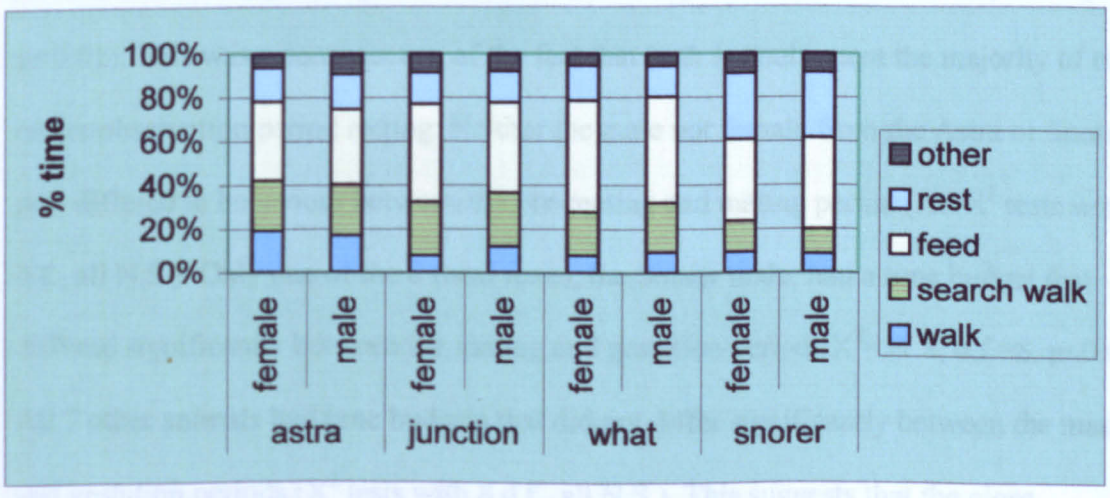

Figure 5.3 Total time budgets of 8 foxes from 4 focal pairs on the study site.

There were no significant differences in time budgets of mated partners (X^2 tests with 3 d.f.; Junction pair X^2=1.5, Astra pair X^2=0.9, Snorer pair X^2=1.0, What pair X^2=0.6. All N.S.). There were however significant differences between the time budgets of individual males (X^2=28, d.f.=12, $p<0.01$) and females (X^2=34.4, d.f.=12, $p<0.01$). For males significant differences lay in the time spent searching for food (X^2=10.11, d.f.=3, $p<0.01$) and resting (X^2=15.2, d.f.=3, $p<0.01$), whereas for females significant differences lay in the time spend walking (X^2=12.9, d.f.=3, $p<0.01$) and resting (X^2=15.5, d.f.=3, $p<0.01$). Males did not differ significantly in the time spent walking, females did not differ significantly in the time spent searching for food, and neither sex differed in the amount of time they spent feeding or performing 'other' activities (X^2 tests with 3 d.f., all N.S.).

A comparison of the time budgets of individual foxes between the pre-mating, mating and gestation periods suggests that their behaviour generally changed little between these periods. Only for the Junction pair did behaviour differ significantly between the pre-mating and mating period (male-X^2= 29.41, d.f.=8, $p<0.01$, female X^2=36.2, d.f.=8, $p<0.01$). This was a consequence of the fact that both animals spent the majority of one entire observation period resting. Neither the male nor female from the Astra or Snorer pair differed in behaviour between the pre-mating and mating period (All X^2 tests with 8 d.f., all N.S.). Only one of the 8 focal foxes, the Snorer male, had a time budget that differed significantly between the mating and gestation period (X^2=11.8, d.f.=8, $p<0.05$). All 7 other animals had time budgets that did not differ significantly between the mating and gestation periods (X^2 tests with 8 d.f., all N.S.). This suggests that the close

proximity partners maintained during the mating period did not carry a cost in terms of reducing feeding rate.

The effect of partner proximity on feeding rate was investigated further by comparing the amount of time foxes spent feeding when they were close to (within 10 m of) or far (>50m) from their partners. This comparison was only possible for the Junction and Astra pairs, because they alone spent significant amount of time together and apart (section 5.3.1). Partner proximity did not significantly affect the feeding rate of either partner in either of these pairs (X^2 tests with 2 d.f., comparing number of observations foxes were seen feeding versus not feeding within 10m of their partners versus further than 50m from their partners, all N.S.).

5.3.4 Do foxes increase their travelling distances during the mating period?

The travelling distances of foxes were compared before, during and after the mating season. If foxes seek extra-pair copulations, we might expect that travelling distances would increase during the mating period.

Table 5.5 shows gives mean travelling distances (per 10 minutes) for the 4 focal fox pairs during the pre-mating, mating and gestation periods. These data reveals that foxes generally moved slowly around their territories, at average speeds of 12.5-18.5 metres per minute.

Table 5.5 Average travelling distances of 4 focal fox pairs before, during and after the mating season. Travelling distances are expressed as the average straight-line distance between locations recorded at 10 minute intervals (for each group n=52 for pre-mating period & n=57 for mating and gestation periods)

	Mean distance travelled (m) during: -			
Group	pre-mating	mating	gestation	totals
Junction	166.6	203.6	185.0	185.6
Astra	172.9	187.1	196.9	186.0
Snorer	144.6	130.3	102.6	125.2
What	-	138.9	98.5	129.3

Analysis of data reveals that there is no significant seasonal variation in distance moved for any of the 4 fox groups (Astra group, $F=0.26$, d.f.=2,163, $p=0.77$; Junction group, $F=0.41$, d.f.=2,163, $p=0.66$; Snorer group, $F=2.07$, d.f.=2,163, $p=0.13$; What group, $t=1.67$, d.f.=111, $p=0.10$). Hence these data provide no evidence to support the prediction that foxes routinely increase or decrease their movement rates during the mating season. Rather the movement rates were found to be relatively constant across the three seasons.

Analysis does however reveal that the average distances travelled does vary significantly between groups (combining all data within groups $F=7.58$, d.f.=3,607, $p<0.001$). This variation does not appear relate simply to territory size, as during this time the What group, which moved an average of 129.3m per 10 minutes, occupied a larger territory than the Astra group, which moved an average of 186m per 10 minutes.

5.3.5 Do foxes alter their ranging behaviour during the mating season?

The home range sizes of males and females were calculated at different stages in the mating season, in order to investigate whether males or females increase their range sizes in the pursuit of extra-pair copulations. 2 comparisons were made, between range sizes: -

1) a) during the 10 weeks leading up to given pairs date of conception, versus
   b) during the females10 week gestation period, and
2) c) during the 10 weeks closest to the main mating period on the study site, and
   d) during the 10 weeks furthest from the main mating period on the study site.

Table's 5.6 and 5.7 show kernel and MCP home range sizes for females and males during these different periods of the mating season. Average values are presented for all data (ranges for individuals tracked over more than one season treated independently) and per individual (range sizes of these individuals averaged to give a single value). These data are also presented graphically in Figures 5.4 and 5.5.

If females increase their range sizes in the pursuit of extra-pair copulations, would predict that their range sizes would be larger in the 10 weeks leading up to their mating period (comparison a. vs b.). Figure 5.4 shows that there is very little variation in female range size according to reproductive state. The only exception to this is female ff19, whose range did increase markedly during the mating period. Unfortunately genetic samples were not obtained from her subsequent litter. Home ranges calculated using Kernel method appear to show even less variation than those calculated using the MCP method, probably because the Kernel technique is less sensitive to outlying data points. Statistical analyses of these data confirm that, on average, female range sizes do not vary significantly with reproductive state using all data (paired t-tests: MCP ranges; a vs b, t=0.34, d.f.=9, p=0.37; c vs d, t=0.70, d.f.=9, p=0.25; Kernel ranges; a vs b, t=0.07, d.f.=9, p=0.47; c vs d t=0.28, d.f.=9, t=0.39) or data averaged per individual (paired t-tests: MCP ranges; a vs b, t=0.05, d.f.=7, p=0.96; c vs d, t=0.1.01, d.f.=7, p=0.34; Kernel ranges; a vs b, t=0.19, d.f.=7, p=0.85; c vs d t=0.41, d.f.=7, t=0.69).

These data therefore provide no evidence that female bat-eared foxes routinely increase their range sizes in the run-up to the mating season. Rather it appears that ranging patterns are relatively constant over the course of the 6 months leading up to parturition.

If males seek extra-pair copulations we would predict that their range sizes should increase during the main mating period on the study site (comparison c. vs d.). Alternatively, if males seek extra-pair copulations after successfully mating with their own partners, we would predict an increase in male range sizes after their partners had conceived (comparison a. vs b.) Figure 5.5 suggests that there is little variation in male range size according to female reproductive state. Statistical analysis shows that, on average, male range sizes do not vary significantly according to female reproductive state for all data (paired t-tests: MCP ranges; a vs b, $t=1.10$, d.f.=9, $p=0.15$; c vs d, $t=0.12$, d.f.=9, $p=0.45$; Kernel ranges; a vs b, $t=0.13$, d.f.=9, $p=0.45$; c vs d $t=0.33$, d.f.=9, $t=0.38$) or data averaged per individual (paired t-tests: MCP ranges; a vs b, $t=0.99$, d.f.=6, $p=0.36$; c vs d, $t=0.38$, d.f.=6, $p=0.71$; Kernel ranges; a vs b, $t=-0.46$, d.f.=6, $p=0.69$; c vs d $t=-0.63$, d.f.=6, $t=0.55$).. These data suggest that male foxes do not wander widely in search of extra-pair copulations.

A potential criticism of this analysis is that 30 radio-tracking fixes may not be sufficient to give an accurate measure of range size. In fact, with this sampling technique employed in this study, 30 fixes probably did give a reasonably accurate measure of range size (see section 2.3.3). Additionally, the analyses presented in this section attempted to investigate relative rather than absolute range sizes.

Table 5.6 Female home range sizes at different times of the breeding season. All ranges calculated using 30 fixes taken from the sample of 60 fixes collected in 6 months up to parturition. Time periods are a) in 10 weeks up to and including females mating period, b) during femaless 10 week gestation period, c) 30 fixes taken closest to main mating period on study site, d) 30 fixes taken furthest from the main mating period on study site.

		Range size (km^2) by time period							
		a		b		c		d	
ID	Year	MCP	Kernel	MCP	Kernel	MCP	Kernel	MCP	Kernel
Ff55	2002	1.75	2.46	1.63	2.28	2.22	2.27	1.51	2.04
Ff16	2001	1.93	1.64	0.91	1.50	1.30	1.62	1.69	1.90
	2002	0.66	0.99	0.78	1.06	0.76	0.85	0.81	1.16
Ff8	2000	1.09	1.66	2.35	3.21	1.74	2.36	1.76	2.70
Ff29	2001	2.73	4.12	2.79	3.08	2.37	3.25	2.76	4.03
Ff46	2002	1.17	1.96	1.92	2.00	2.09	2.71	1.36	1.62
Ff19	2000	3.47	3.82	2.20	3.51	4.37	4.83	2.04	3.68
Ff30	2001	1.16	1.37	1.06	1.24	1.19	1.47	1.25	1.41
Ff28	2001	2.05	2.13	1.79	1.88	1.23	2.03	2.10	2.02
	2002	1.61	2.18	1.34	1.85	1.47	1.43	1.32	2.06
All data	$\bar{x}$	1.76	2.33	1.68	2.35	1.85	2.43	1.64	2.37
	s.d.	0.82	1.01	0.65	0.85	1.04	1.13	0.56	0.94
Per	$\bar{x}$	1.81	2.36	1.80	2.31	2.03	2.48	1.70	2.38
individual	s.d.	0.87	1.07	0.65	0.87	1.08	1.16	0.51	1.00

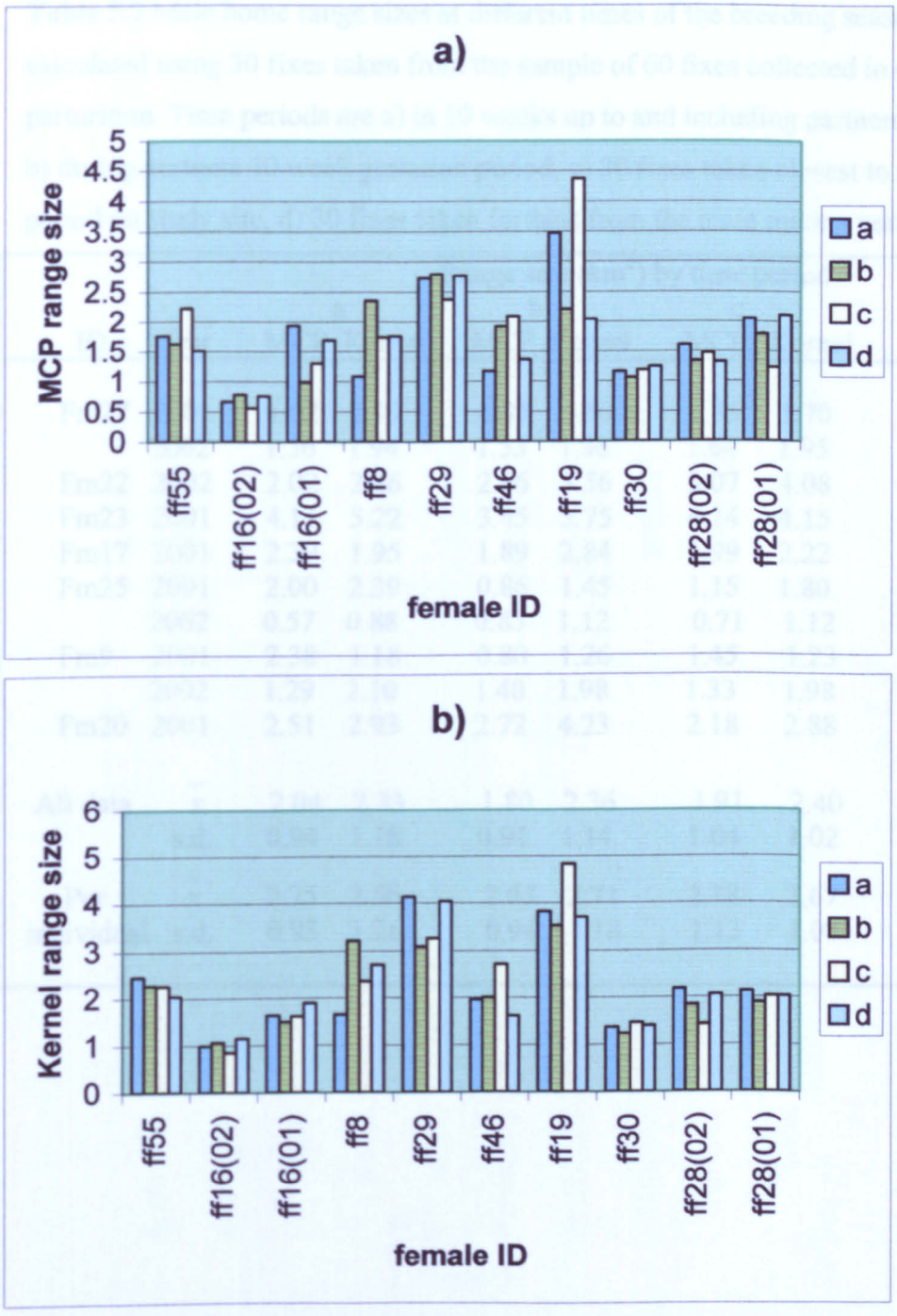

Figure 5.4 Female home range sizes (km^2) for the 4 time periods calculated using a) MCP and b) Kernel method. Time periods are a) 30 fixes from10 weeks up to and including the females mating period, b) 30 fixes from 10 week gestation period, c) 30 fixes either side of mating period, d) 30 fixes furthest from mating period.

Table 5.7 Male home range sizes at different times of the breeding season. All ranges are calculated using 30 fixes taken from the sample of 60 fixes collected in 6 months up to parturition. Time periods are a) in 10 weeks up to and including partners mating period, b) during partners 10 week gestation period, c) 30 fixes taken closest to main mating period on study site, d) 30 fixes taken furthest from the main mating period on study site.

		Range size (km^2) by time period							
		a		b		c		d	
ID	Year	MCP	Kernel	MCP	Kernel	MCP	Kernel	MCP	Kernel
Fm27	2001	1.62	2.19	1.85	1.50	1.35	1.70	2.12	1.96
	2002	1.56	1.94	1.53	1.96	1.64	1.95	1.31	1.88
Fm22	2002	2.02	2.46	2.66	3.56	3.07	4.08	2.42	3.66
Fm23	2001	4.11	5.22	3.45	3.75	4.24	4.15	3.91	4.15
Fm17	2001	2.39	1.95	1.89	2.84	1.99	2.22	3.27	2.52
Fm25	2001	2.00	2.39	0.86	1.45	1.15	1.80	2.23	2.06
	2002	0.57	0.88	0.83	1.12	0.71	1.12	0.64	1.02
Fm9	2001	2.38	1.18	0.80	1.26	1.45	1.23	0.95	1.00
	2002	1.29	2.10	1.40	1.98	1.33	1.98	1.93	1.83
Fm20	2001	2.51	2.93	2.72	4.23	2.18	2.88	3.32	3.61
All data	$\bar{x}$	2.04	2.33	1.80	2.36	1.91	2.40	1.89	2.48
	s.d.	0.94	1.18	0.91	1.14	1.04	1.02	0.95	1.59
Per	$\bar{x}$	2.25	2.56	2.05	2.71	2.18	2.67	2.13	2.88
individual	s.d.	0.93	1.26	0.94	1.18	1.13	1.08	0.96	1.73

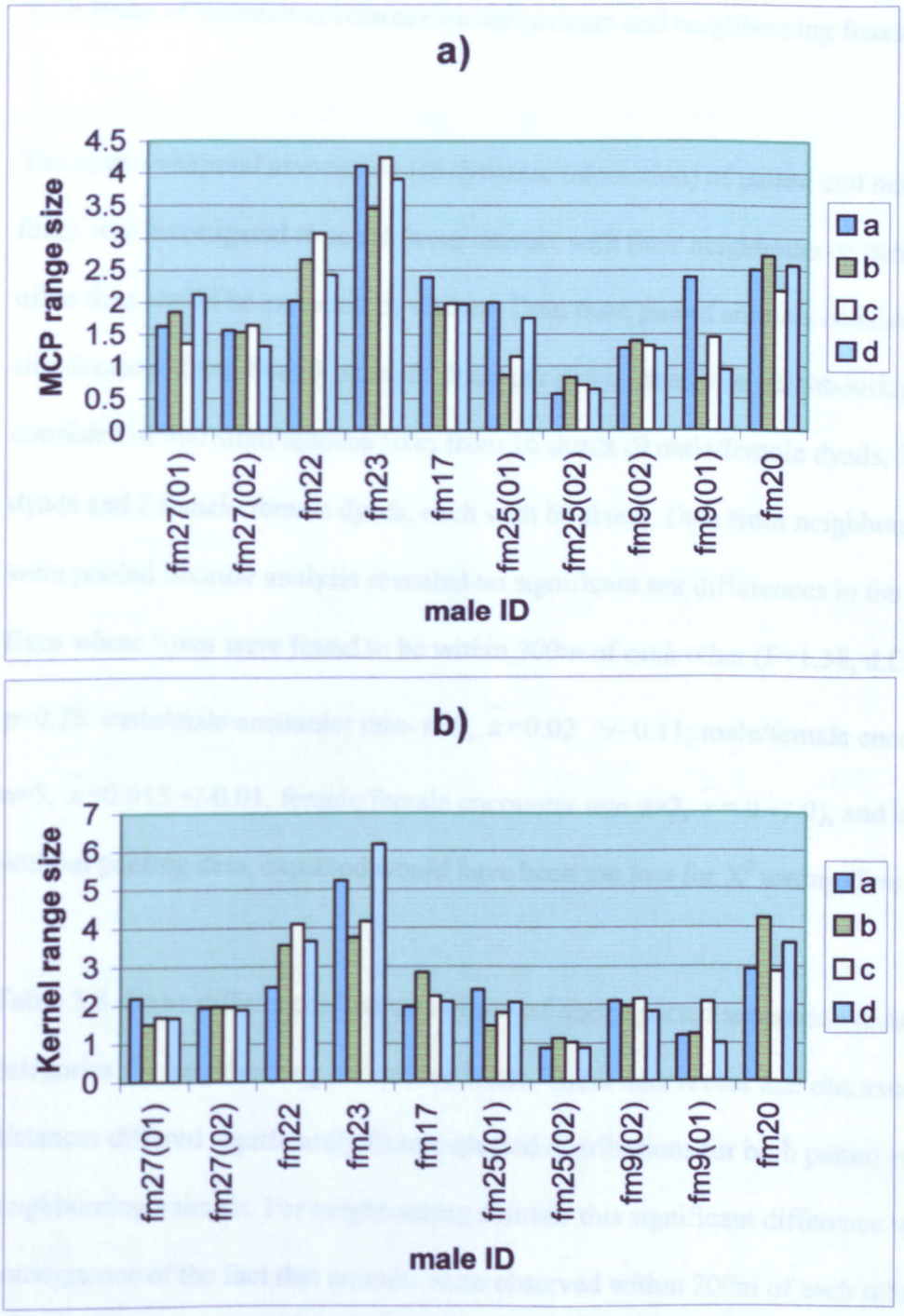

Figure 5.5 Male home range sizes (km^2) for the 4 time periods calculated using a) MCP and b) Kernel method. Time periods are a) 30 fixes from10 weeks up to and including the females mating period, b) 30 fixes from 10 week gestation period, c) 30 fixes closest to the mating period on the study site, d) 30 fixes furthest from mating period.

5.3.6 Rates of interaction between mated partners and neighbouring foxes

The spatio-temporal association (or dynamic interaction) of paired and neighbouring foxes was investigated to see if foxes interact with their neighbours or partners more often than would be expected by chance. Data from paired animals consisted of 180 simultaneous fixes from 3 pairs (60 fixes per pair). Data from neighbouring animals consisted of 960 simultaneous fixes from 16 dyads (9 male/female dyads, 5 male/male dyads and 2 female/female dyads, each with 60 fixes). Data from neighbouring dyads were pooled because analysis revealed no significant sex differences in the proportion of fixes where foxes were found to be within 200m of each other ($F=1.38$, d.f.=2,13, $p=0.28$: male/male encounter rate- n=9, $\bar{x}=0.02$ +/- 0.11; male/female encounter rate, n=5, $\bar{x}=0.015$ +/-0.01, female/female encounter rate n=2, $\bar{x}=0$ +/-0), and because, without pooling data, expected would have been too low for X^2 testing (less than 1).

Table 5.8 shows differences between observed and expected separation distance categories for neighbouring and paired foxes. These data reveal that observed separation distances differed significantly from expected distributions for both paired and neighbouring animals. For neighbouring animals this significant difference was a consequence of the fact that animals were observed within 200m of each other more than twice as often as would have been expected by chance (for all other separation distances observed and expected values were similar). For paired animals this difference was a consequence of the fact that partners were almost always found within 200m of each other (as was shown by behavioural data presented in section 5.3.1.)

Table 5.8 Frequencies of observed and expected separation distances of neighbouring and paired animals obtained from simultaneous radio-tracking fixes. Comparisons were made using one sample X^2 with frequencies from observed and expected values. All tests have 3 d.f.

Group encounters	Separation distance categories (m) 0-199	200-399	400-599	600+	Total X^2	Significance (p)
Inter-group						
observed data	14	26	41	875		
expected data	6.55	23.25	39.5	888.56		
partial X^2	8.47	0.33	0.06	0.21	9.07	<0.05
Intra-group						
observed data	159	5	2	7		
expected data	15.68	32.3	38.4	89.6		
partial X^2	1309.7	23.07	34.55	76.12	1433.5	<0.001

Table 5.9 Frequencies of observed and expected observations of separation distances within and beyond 200m for neighbouring and paired animals during 10 weeks up to and including the mating period and during the 10 week gestation period.

	up to mating period <200m	200m +	X^2	p	gestation period <200m	200m+	X^2	p
Inter-group								
observed data	11	469			3	477		
expected data	3.41	476.59			3.48	476.52		
partial X^2	16.89	0.12	17.01	<0.001	0.07	0.004	0.07	N.S.
Intra-group								
observed data	87	3			75	15		
expected data	6.03	83.97			7.69	82.31		
partial X^2	1087	78.08	1165	<0.001	589.1	55.04	644.1	<0.001

The dynamic interaction between paired and neighbouring foxes was investigated further by comparing the frequency with which neighbours and partners were found within 200m of each other during the 10 weeks leading up to the mating season versus during the 10-week gestation period (Table 5.9).

Data presented in Table 5.9 shows that neighbouring foxes differed significantly from an expected distribution only in the run up to the mating season, when they were found within 200m of each other approximately 3 times more often than was expected by chance. During the gestation period observed separation distances were very similar to those expected by chance. A 2x2 comparison of observed separation frequencies differ significantly between the run up to the mating period versus during the gestation period (X^2=4.65, d.f.=1, $p<0.05$).

Paired animals were found within 200m of each other significantly more often than expected during both the run up to the mating season and during the gestation. However, a 2x2 comparison of observed separation distances during the two time periods reveals that partners were found together significantly more often in the run-up to the mating season than they were during the gestation period (X^2=8.89, d.f.=1, $p<0.001$). Behavioural data presented in section 5.3.1 suggested a similar pattern.

5.4 Discussion

5.4.1 Partner proximity and mate guarding

Data on partner proximity presented in section 5.3.1 shows there is a degree of flexibility in the extent to which bat-eared foxes associate with their partners during the pre-mating, mating and gestation periods. Two focal pairs (Snorer & What) did not adjust their behaviour by season, but maintained similarly high levels of proximity during and outside the mating season (although the what pair was not observed during the pre-mating period). By contrast two of the focal pairs (Junction & Astra) adjusted their behaviour by season, maintaining close proximity during the mating period (within 10 m of each other on 85 and 90% of observations respectively), but being found apart significantly more often during the pre-mating and gestation periods. These pairs differed in the extent to which partners associated during the pre-mating and gestation periods, with the Astra pair being found more than 200m apart on approximately 50 % of observations, and the junction pair being found more than 200m apart on approximately 25 % of observations.

Data presented in section 5.3.2 suggests that the degree to which males and females were responsible for maintaining proximity with their partners across seasons was not always consistent with a male mate guarding strategy. Only in one of the two-pairs in which partners increased proximity during the mating period (the Astra pair) was the male responsible for this increase. Similarly, only in one of two pairs in which partners

maintained close proximity across time periods (the Snorer pair) did the male follow his partner more than expected by chance. This may reflect the fact that the costs and benefits of engaging in extra-pair copulations could vary between females, according to the quality of their partners. For females paired to high quality males, extra-pair matings may be more costly than they are beneficial. Under these circumstances males and females have a mutual interest in maintaining close proximity during the females fertile period (Petrie & Kempenaers 1998).

Data presented in section 5.3.3 suggests that there is little cost to bat-eared fox partners in maintaining close proximity during the mating period. Firstly, there was no evidence that feeding rates dropped during the mating season, and secondly there was no association between partner proximity and feeding rate (c.p. Komdeur 2001). Indeed the fact that two fox pairs maintain close proximity outside of the mating period suggests that the strategy carries advantages other than the promotion of mating fidelity. It may be that the depletion and renewal rates of the foxes termite prey make it advantageous for foxes to feed in pairs rather than singly (see Davies & Houston 1992). Alternatively or additionally, foraging in pairs may reduce predation risk. Whatever the case, the fact that some pairs almost always forage together while others often foraged apart suggests that, for this population, there is a fine balance between the advantages and disadvantages of the two strategies.

5.4.2 Do bat-eared foxes expand their ranges during the mating season?

Data presented in section 5.3.5 suggests that neither males nor females routinely adjust their ranging behaviour during the mating period. If males adopted the mixed reproductive strategy suggested by Trivers (1972), we might predict that their home range sizes would increase after their partners had conceived. There was no evidence that this occurred (comparison a vs. b Figure 5.5). If females increase their range sizes in the pursuit of extra-pair copulations we might similarly predict an increase in female range size prior to conception (comparison a vs. b, Figure 5.4). Again, there was no evidence to support this prediction (although one female, ff19, did markedly increase her range size during this period). In fact these data suggest that range sizes of both males and females remained relatively constant across these periods. It therefore appears that, unlike some other species of fox (section 5.1.4), neither males nor female bat-eared foxes routinely adopt roaming strategies during the mating season.

One reason why male (and female) bat-eared foxes may not adopt such a 'roaming' strategy is that time constraints imposed by their termite eating diet may prevent them from doing so. Overall time budgets (Figure 5.3) reveal that foxes spend the vast majority of the night actively foraging. 3 of the 4 focal fox pairs spent approximately 15 % of their night resting (or 1 hour and 40 minutes of an 11 hour night). This suggests that bat-eared foxes have little time to engage in activities other than foraging, and that the adoption of a roaming strategy during the mating season could interfere with normal foraging and potentially carry a high energetic cost. Stanback *et al.* (2002) have similarly suggested

that time/energy constraints might prevent desert living Monteiros hornbills from seeking extra-pair copulations, because the benefits of mating (and conceiving) outside the pair bond would never compensate for high energetic costs (see also Palokangas *et al.* 1992).

5.4.3 Does this mean that bat-eared foxes are unlikely to engage in extra-pair copulations?

The fact that bat-eared foxes don't roam during the mating season might lead one to conclude that bat-eared foxes never engage in extra-pair copulations. However, data presented in sections 4.3.2 and 5.3.6 show that bat-eared fox ranges often overlap considerably with those of their neighbours, and that neighbours often meet up in areas of shared territory. This suggests that the bat-eared foxes normal ranging patterns provide individuals with the opportunity to meet up with and assess neighbours as potential extra-pair copulation partners. Moreover, the fact that neighbours were found close together significantly more often in the run-up to and during the mating season than during the gestation period (Table 5.9) suggests that these could represent encounters by males or females attempting to assess potential mates and engage in extra-pair copulations.

In order to understand the biological relevance of these results, however, it is necessary to consider whether instances where foxes are found within 200m of each other represent real interactions (i.e. that one or both of the animals involved were at least aware of the others presence). Macdonald *et al.* (1980) estimate that foxes are mutually capable of perceiving each other from distances of 50-100m. In the open habitat on the bat-eared fox

study site this figure may be slightly higher, but probably not high enough that foxes can detect neighbours from 200m away.

One way of addressing whether or not foxes actually 'interact' with neighbours significantly more often than is expected by chance is to calculate the minimum separation distance over which the significant association holds. For the significant association to have existed in the run-up to the mating season, 8 within 200m interactions would have to have occurred. 8 of the 11 observed interactions occurred within distances of 125 m, and 9 within 135m. Both of these distances are less than the mean error of radio-tracking fixes obtained in this study (141m, see section 2.3.1). This tentatively suggests that a sufficient number of 'interactions' to provide a statistically significant result probably did represent instances when at least one of the two foxes was aware of the neighbour's presence. Having said this, a proportion of these interactions may have taken place between neighbouring kin (appendix 4.1), who foxes may avoid mating with.

5.4.4 Summary

Evolutionary theory predicts that monogamous males and females can both gain by mating with individuals other than their social partners. This chapter presents behavioural and radio-tracking data investigating if and why bat-eared foxes seek to mate outside the pair bond.

I found that the behaviour of mated bat-eared fox partners is highly co-ordinated. Although there is variation between pairs, bat-eared foxes generally spend most of the night foraging close to their partners. Levels of proximity are particularly high during the mating season, when all fox pairs observed spent the majority of their time within 5 metres of their partners. This suggests that it could be difficult for bat-eared fox females to mate with individuals other than their social partners.

For some pairs the high levels of proximity maintained during the mating period were attributable to male mate guarding (males were primarily responsible for maintaining proximity), but for other pairs this was not the case. This suggests that females and males benefit from staying close to their partners, both during and outside of the mating season.

Foxes spend the vast majority of their time actively foraging, and therefore have little time to engage in alternative activities. This suggests that the pursuit of extra-pair copulations could carry a high energetic cost. By contrast the maintenance of close partner proximity does not appear to carry an energetic cost, as feeding rates did not decrease during the mating season, and their was no association between feeding rate and partner proximity. Together these facts predict that bat-eared foxes may be unlikely to pursue extra-pair copulations.

Consistent with this prediction radio-tracking data reveals that bat-eared fox males, unlike males of some other fox species, do not wander widely during the mating season. This might lead one to conclude that extra-pair copulations are very unlikely to occur in

the species. However, bat-eared foxes regularly interact with neighbours in areas of shared territory, particularly in the run-up to the mating season. This suggests that they may be able to assess potential extra-pair mates and engage in extra-pair copulations without altering their usual ranging patterns, and demonstrates that both behavioural and genetic data are required for a comprehensive understanding of a species social behaviour (Hughes 1998).

Chapter 6

DNA microsatellite analyses of paternity of fox cubs- are bat-eared foxes genetically monogamous?

6.1 Introduction

6.1.1 Multiple mating and multiple paternity in mammals

There are a number of ways in which females from both socially monogamous and non-monogamous species can increase their fitness by mating with more than one male (see section 5.1.1, reviewed by Gomendio *et al.* 1998). In line with this, there is now clear behavioural evidence of multiple mating by female mammals from a wide range of taxa (reviewed by Ginsberg & Huck 1989). As has been demonstrated in birds (section 5.1.1), field data reveal that females of some mammal species actively seek multiple mates (Hanken & Sherman 1981, Agren 1990, Betreaux *et al.* 1999).

While multiple mating may not necessarily result in multiple paternity (this depends on the timing of mating in relation to the timing of ovulation, e.g. see Hunter *et al.* 1992), numerous mammalian studies have demonstrated multiple paternity in using genetic techniques (in rodents- Burton 2002, primates- Radespiel *et al.* 2002, marsupials Kraaijeveld-Smit *et al.* 2002, see also Stockley 2003). Rather amazingly, multiple mating

may be the rule rather than the exception among carnivores, as it has been reported (albeit sometimes at low rates) in every carnivore species on which genetic tests have been carried out (reviewed in Creel & Macdonald 1995, see also Craighead *et al.*1995, Schenk & Kovaks 1995, Gompper *et al.* 1997, East *et al.* 2003 and refs in Table 6.1).

6.1.2 Mating behaviour of monogamous mammals

Relatively few data are available on the mating behaviour of monogamous mammals, and it remains to be seen if they are generally as promiscuous as their avian counterparts. Having said this, extra-pair copulations have been observed in at least 6 species of socially monogamous mammal (see section 5.1.3). Assessments of parentage based on genetic data have been carried out on 13 species reported to be socially monogamous (on the basis that males and females form pairs, defend a common territory and interact preferentially, sometimes in the presence of related subordinates). Levels of extra-pair paternity found in these studies are shown in Table 6.1. These studies demonstrate that socially monogamous mammals, like their avian counterparts, exhibit an array of genetic mating systems.

In four of the five species of monogamous rodent tested, extra-pair paternity was absent. The exception was the Alpine Marmot, a species in which monogamous pairs live with extended family groups. In this species 19 % of young (in 31.4% of litters) were not sired by their putative fathers. Paternity could not be assigned to subordinate (within group) or

Table 6.1. Summary of genetic data on mating behaviour of 13 species of monogamous mammal. Levels of extra-pair paternity reported are % of offspring sampled.

species	scientific name	reported levels of EPP	reference
Kirk's dik dik	*Madoqua kirkii*	absent	Brotherton *et al.* 1997
Oldfield mouse	*Peromyscus polionotus*	absent	Foltz 1981
California mouse	*Peromyscus californicus*	absent	Ribble 1991
Deer mouse	*Peromyscus maniculatus*	absent	Ribble & Millar 1996
Alpine Marmot	*Marmota marmota*	19%	Goosens *et al.* 1997
Giant jumping rat	*Hypogeomys antimena*	absent	Sommer & Tichy 1999
Allied rock wallaby	*Petrogale assimilis*	33%	Spencer & Marsh 1997
Lesser woolly-Horseshoe bat	*Rhinolophus sedulus*	absent	Heller *et al.* 1993
Fat-tailed dwarf lemur	*Cheirogaleus medius*	44%	Feitz *et al.* 2000
Alaotran gentle lemur	*Hapalemur griseus*	8%	Neveu *et al.* 1996
Island fox	*Urocyon littoralis*	25%	Roemer *et al.* 2001
Ethiopian wolf	*Canis simensis*	see text	Sillero *et al.* 1996
African wild dog	*Lycaon pictus*	10%	Girman *et al.* 1997

resident neighbouring (extra-group) males, suggesting that satellite males must have fathered some extra-pair offspring.

Genetic data on parentage are available for 3 canid species, 2 of which live in packs consisting of a dominant pair and related subordinates. In the African wild dog, subordinate males from within the same pack sired 10% of offspring (Girman *et al.* 1997). In the Ethiopian wolf, extra-group copulations are more common than within-pair copulations, and did result in multiple paternity (in 2 of 9 litters- Sillero *et al.* 1996). In this species females may seek extra-group copulations to avoid inbreeding, as the dominant pair may often be close relatives. This may come about because a shortage of suitable habitat reduces dispersal options. The island fox is the only small canid for which genetic paternity data is available. In this species 25 % (4 of 16) of offspring tested had been sired by males other than their social father (Roemer *et al.* 2001).

At present there are no obvious behavioural or ecological factors that explain observed variation in EPP among monogamous mammals. Certainly though, genetic monogamy is not necessarily associated with a requirement for male care. For example, fat-tailed dwarf lemurs exhibit the highest levels of extra-pair paternity recorded among monogamous mammals, despite the expression and apparent requirement for paternal care (Fietz 1999). In contrast, male dik-diks, which provide no care for their offspring (Brotherton & Rhodes 1996), have been found to be strictly genetically monogamous.

What do monogamous female mammals gain from mating with individuals other than their social partners? Because of the (uneven) distribution of extra-pair paternity between litters, Goosens *et al.* (1997) suggest that female Alpine Marmots seek to mate with individuals who are of superior genetic quality to their partners (as often appears to be the case in birds- section 5.1.1). In Ethiopian wolves, on the other hand, covert extra-pair mating may well function as an inbreeding avoidance mechanism (see above). A recent comparative study of the mating behaviour of female mammals (not just socially monogamous ones), however, suggests that the main function of multiple mating by females may be to reduce the risk of mating (only) with an infertile or incompatible mate (Stockley 2003).

6.1.3 Aims of chapter

Behavioural data presented in the previous chapter show that neither male nor female bat-eared foxes roam widely during the mating season (section 5.3.5). Additionally, males remain close to their partners during the mating season, and there appears to be little or no cost to this behaviour (section 5.3.1). These facts might lead one to predict that EPP are likely to be absent or low in this population of bat-eared foxes. However, the observation that the ranges of neighbouring pairs often overlap extensively, and that neighbours regularly meet on areas of common ground (particularly in the run up to the mating season- section 5.3.6) suggests that this may not be the case. Clearly genetic data are required to resolve the question of whether bat-eared foxes are genetically monogamous.

This chapter presents the first data establishing the genetic parentage of bat-eared fox cubs, and aims to establish what proportion of cubs (if any) are sired by extra-pair males.

6.2 Methods

6.2.1 Collection of samples

Adult foxes and cubs were captured using the methods described in section 2.2. When fitting ear-tags to adult foxes, the small piece of tissue made by the ear punch was collected for DNA analysis. DNA samples were collected from cubs by snipping off the smallest possible quantity of tissue from their tail tips. All tissue samples were stored in TES buffer (100mM Tris HCl, 100mM EDTA, 2 % sodium dodecyl sulphate) at room temperature.

A total of 73 animals were used in the paternity analysis. This sample included 44 cubs for which both mother and social father had been captured (12 males and 11 females from 11 pairs, with 1 female having repaired). A further 6 animals (5 males and 1 female) were captured on the study site, 4 of which (3 males and 1 female) formed part of a resident pair at some point, and 2 of which (both males) were single floaters.

6.2.2 Laboratory techniques

Analysis of samples was carried out by Melissa Gray at the University of California Los Angeles, using the following protocol: -

DNA Extraction

Genomic DNA was extracted from each tissue sample using the QiaAmp DNA blood mini kit from Qiagen. 30ul of the sample was stored at 4 °C as a working sample while the remainder was stored at –80 °C.

Choice of microsatellite markers

Individuals were genotyped using 13 microsatellite primers for which bat-eared foxes were found to be polymorphic. Nine of these were dinucleotide primers developed by Goldstein *et al.* (1999) for work on island foxes. The remaining 4 were tetra-nucleotide primers developed for domestic dogs (by the Fred Hutchinson Cancer Research Centre dog genome project). Details of these primers, the number of alleles found at each locus, and hetrozygosity estimates for each locus are given in Table 6.2.

DNA amplification

Fluorescents dye labelled primers were ordered from Operon Technologies. One labelled and one unlabelled primer (20pmol) were added to 50 ng genomic DNA, 0.2 mM dNTP, 2.5 mM $MgCl_2$, 1X DNA reaction buffer, and 0.8 units of Taq DNA polymerase (Promega) in a reaction volume of 25µl. An Eppendorf Mastercycler thermalcycler was used for PCR amplification. An initial denaturation was performed at 94°C for 5 minutes (min), followed by 30 cycles of denaturation at 94°C for 45 sec, annealing at 54-62°C for 45 sec (annealing temperatures were optimized for each primer pair), and extension at 72°C for 1 min. A final extension period at 72°C for 5 min was performed at the end of

Table 6.2 Details of the 13 microsatellite primers used in the paternity analysis. Hetrozygosity estimates are based on 73 individuals sampled on the main study site.

locus	forward & reverse primer	fluorescent label used	number of alleles	% heterozygosity
di-nucleotide				
147	CCATGGGAAACCACTTGC ACTTCATCATGTCTGGAAGCG	HEX	3	52
250	TTAGTTAACCCAGCTCCCCCA TCACCCTGTTAGCTGCTCAA	FAM	7	44
279	TGCTCAATGAAATAAGCCAGG GGCGACCTTCATTCTCTGAC	HEX	4	42
366	ACATCCTCCCTCTAGCACCA TCCCCACTGCTCATTCTCTT	HEX	4	62
377	ACGTGTTGATGTACATTCCTGC CCACCCAGTCACACAATCAG	FAM	8	68
410	GAGGAAAACCAAGTGATTTTGG ACCTGCAAGTGACCCTCTCT	FAM	3	57
431	CATGCATGTGAGGACTGATTG CACAACCAGAGGGTTTCAAA	HEX	10	77
606	AAAGGCTGTGGAATTAATGTGA AATTCCTTGCTTGCTATCAAAA	FAM	5	74
671	AAAATGAAAAAGGAAGAGAGGG AGGAGACAGGATTTTCCTCTCA	HEX	5	58
tetranucleotide				
2140	GGGGAAGCCATTTTTAAAGC TGACCCTCTGGCATCTAGGA	FAM	14	80
2293	GAATGCCCTTCACCTTGAAA AGGAAAAGGAGAGATGATGCC	HEX	10	80
PEZ 17	CTAAGGGACTGAACTTCTCC GTGGAACCTGCTTAAGATTC	HEX	2	28
PEZ 19	GACTCATGATGTTGTGTATC TTTGCTCAGTGCTAAGTCTC	HEX	5	41

the 30 cycles. After the completion of the PCR amplification, the samples were stored at 4°C until sequencing was performed.

Scoring genotypes

Fluorescent-labelled PCR products were run on a ABI3700 (capillary system) sequencer (Applied Biosystems Inc.). Pairs of loci were pooled together and diluted 1:10. Then, in each well, 2 μl of pooled product was combined with 9.7 μl of formamide and 3 μl of Liz size standard. This loading mix was denatured (at 95°C for five minutes) and then run on the sequencer. Genotypes were determined using GENOTYPER analysis software (Applied Biosystems Inc.), which compares the location of the fluorescent microsatellite fragment to the fluorescent size standard.

6.2.3 Assignment of parentage

Paternities were examined using the likelihood approach implemented by the program CERVUS 1.0 (Marshall *et al.* 1998). This program works by first computing allele frequencies at each locus under investigation. Based on these allele frequencies, and the genotypes of offspring, known mothers, and potential fathers, the program then calculates a log-likelihood score (LOD score, after Meagher 1986) for each candidate father. A statistic Δ is then determined, which is equal to the difference in LOD scores between the most likely candidate parent and the second most likely candidate parent. The statistical significance of the Δ score is determined by comparing observed delta scores with those obtained by a simulation model. For a large number of simulated parentage tests (10000),

this model compares the distribution of delta's for tests in which the most likely candidate parent was the true parent with the distribution of delta scores for tests in which the most likely candidate parent was not the true father.

CERVUS assigns four levels of confidence to paternities of potential fathers. These are i) strict confidence, ii) relaxed confidence, iii) most likely parent, and iv) nothing. Strict confidence is given to a parent that is found to be the true parent with 95% likelihood. Relaxed confidence is given to a parent that is found to be the true parent with at least 80% likelihood. The "most likely" term is given to a parent that is found to be most likely the true parent, but does not fall within the relaxed confidence level, and the last category is given to fathers that can be excluded as potential parents (less than 5 % chance of being a true parent).

In comparison with traditional paternity exclusion analyses, likelihood techniques have a number of advantages (Marshall *et al.* 1998, Slate *et al.* 2000). These include the fact that it takes into account the effects of typing error, missing genotypes and un-sampled candidate males. Marshall *et al.* (1998) point out that paternity assigned with 80% confidence is often more accurate than estimates obtained using a purely exclusionary approach. In their test sample 80% confidence corresponded to a median exclusion probability of 0.9998.

6.3 Results

Results of the paternity analysis are presented in Table 6.3. This table show the results of 2 analyses (run using CERVUS). Both analyses allowed CERVUS to choose a cub's most likely candidate father (based on the genotypes of the cub, known mothers and potential fathers), and calculate the degree of certainty with which paternity could be assigned to this male. In the first analysis we used data from all 13 microsatellite loci (Table 6.2). In the second analysis data from 2 loci (147 & 2140) were not used, because both loci deviated significantly from Hardy-Weinberg equilibrium, and locus 147 had a high probability of null alleles (both resulting in a reduced the reliability of data– Marshal *et al.* 1998).

Results of the 2 analyses were very similar. For the majority of cubs, paternity was confidently assigned to social fathers. In the first analysis, paternity was assigned to social fathers with strict (95%) confidence for 26 of 44 (59.1 % of) cubs, with relaxed (80%) confidence for 36 of 44 (or 81.8 % of) cubs, and with lower confidence (most likely parent) for 42 of 44 (95.5 % of) cubs. In the second analysis, paternity was assigned to social fathers with strict confidence for 29 of 44 (65.9 % of) cubs, with relaxed confidence for 37 of 44 (84.1 % of) cubs, and with lower confidence for 42 of 44 (95.5 %) of cubs.

Both analyses suggested that two cubs were sired by males other than their social fathers. These cubs, ff62 & fm76, were born into different litters of the Astra female, ff28. For

Table 6.3 Paternity of 44 bat-eared fox cubs (from 15 litters of 11 fox pairs) established by DNA microsatellite analysis. The table gives the group name and litter year, as well as the ID numbers of cubs, mothers and putative (social) fathers. The results of 2 paternity analyses (see text) are shown, both of which identify each cub's most likely father, and the confidence that this animal was the true father.

					Analysis 1		*Analysis 2*	
Group	Litter year	cub	mother	social father	father	confidence	father	confidence
Reflector	2000	f7	ff8	fm6	fm6	80%	fm6	most likely
Ghost	2001	ff39	ff46	fm9	fm9	80%	fm9	most likely
		ff40	ff46	fm9	fm9	95%	fm9	95%
		fm41	ff46	fm9	fm9	95%	fm9	95%
	2002	ff78	ff46	fm9	fm9	95%	fm9	95%
		ff79	ff46	fm9	fm9	95%	fm9	most likely
Snorer	2000	fm26	ff16	fm15	fm15	80%	fm15	80%
	2001	fm64	ff16	fm25	fm25	80%	fm25	80%
		fm65	ff16	fm25	fm25	most likely	fm25	most likely
		ff77	ff16	fm25	fm25	most likely	fm25	80%
Everest	2001	fm52	ff62	fm20	fm20	95%	fm20	95%
		fm53	ff62	fm20	fm20	80%	fm20	80%
		ff60	ff62	fm20	fm20	80%	fm20	80%
		ff63	ff63	fm20	fm20	80%	fm20	80%
Mzee	2001	ff61	ff70	fm23	fm23	95%	fm23	95%
		fm71	ff70	fm23	fm23	95%	fm23	95%
		fm72	ff70	fm23	fm23	80%	fm23	80%
		ff73	ff70	fm23	fm23	95%	fm23	95%
Junction	2001	ff48	ff29	fm22	fm22	95%	fm22	95%
		fm49	ff29	fm22	fm22	95%	fm22	95%
		fm50	ff29	fm22	fm22	95%	fm22	95%
		ff51	ff29	fm22	fm22	95%	fm22	95%
Astra	2000	ff62	ff28	fm27	**fm9**	most likely	**fm9**	most likely
	2001	fm75	ff28	fm27	fm27	most likely	fm27	most likely
		fm76	ff28	fm27	**fm25**	most likely	**fm9**	most likely
Grebe	2001	ff34	ff33	fm32	fm32	95%	fm32	95%
		ff35	ff33	fm32	fm32	80%	fm32	95%
		fm36	ff33	fm32	fm32	most likely	fm32	95%
		fm37	ff33	fm32	fm32	95%	fm32	95%
		ff38	ff33	fm32	fm32	most likely	fm32	95%
Neils	2001	fm42	ff68	fm31	fm31	95%	fm31	95%
		ff43	ff68	fm31	fm31	most likely	fm31	95%
		fm44	ff68	fm31	fm31	95%	fm31	95%
		ff66	ff68	fm31	fm31	80%	fm31	80%
		fm67	ff68	fm31	fm31	95%	fm31	95%
What	2001	fm56	ff55	fm54	fm54	95%	fm54	95%
		fm57	ff55	fm54	fm54	95%	fm54	95%
		ff58	ff55	fm54	fm54	95%	fm54	95%
		ff59	ff55	fm54	fm54	95%	fm54	95%
	2002	fm80	ff55	fm54	fm54	95%	fm54	95%
		ff81	ff55	fm54	fm54	95%	fm54	95%
		ff82	ff55	fm54	fm54	95%	fm54	95%
		fm83	ff55	fm54	fm54	95 %	fm54	95%
Puffadder	2001	ff69	ff47	fm17	fm17	95%	fm17	95%

one cub (ff62), the resident male from the neighbouring Ghost pair (fm9) was identified as a possible candidate father (with low confidence). For the other cub (fm76), the male from the Snorer pair (fm25) was identified as a potential candidate father (again with low confidence). Regardless of the fact that paternity of these cubs was not confirmed with high confidence, fm27 was excluded as a potential father of either cub. For both cubs (and in both analyses), fm27 was incompatible as a potential father at 5 loci. Given the degree of error in the data (calculated by looking at mismatches in the genotypes of cubs and known mothers), it is very unlikely that this degree of genetic dissimilarity would occur between offspring and true parents (even for the 5 loci with highest error rate, the chance of this occurring would be extremely low- $p<0.0001$).

Variations in the degree of confidence attached to paternity reflect variation in the number of mismatching alleles occurring between fathers and cubs, and the number of other males who were not excluded as potential fathers. Mismatches between offspring and true parents can occur for a number of reasons, including through mutation, typing error, and the presence of null alleles (Marshall *et al.* 1998). It is worth noting that the genotypes of males identified as 'most likely' parents were only ever incompatible with offspring at 1 or 2 loci, and that this number of mismatches sometimes occurred between cubs and known mothers. This illustrates the point that 'most likely' fathers had a good chance of being true parents.

Overall, theses data demonstrate a high degree of genetic monogamy among bat-eared foxes on the study site, with 42 of 44 (95.5% of) cubs apparently being sired by their

social fathers. Extra-pair paternity occurred at a low level, with 2 of 44 (4.5 %) of cubs very likely to have been sired males' other than their social fathers. Extra-pair paternity was found to occur in 9.1 % (1 of 11) of pairs (and females), and 13.3 % (2 of 15) of litters.

6.4 Discussion

6.4.1 The genetic mating system of the bat-eared fox

Data presented in this chapter demonstrate a high degree of genetic monogamy in the study population, with only 2 of 44 (or 4.5%) of the cubs apparently being sired by males other than their social fathers.

Although they were born in different litters, both 'extra-pair cubs' were sired by the same female, ff28. In ff28's 2001 litter, the female's social partner, fm27, was the most likely father of a second cub sampled. This strongly suggests that multiple paternity occurred within a single litter, and therefore that female ff28 mated with at least 2 males during a single oestrous period.

Two male residents on the study site were identified as potential fathers of ff28's extra-pair cubs (although not with a high degree of certainty). One of these males, fm9, was a neighbour with a large degree of home range overlap (section 4.3.2). Indeed, around the time of the 2001 mating season, this 'pair' of animals were found interacting in an area of shared territory (although cub ff62 was conceived the previous year). A second male, fm25, was identified as a potential father of the 2nd extra pair cub, fm76. This male was not an immediate neighbour of ff28, but lived 2 territories away. These animals were never found in the same area (their closest recorded locations were 540m away), so if

fm25 was the true father this cub, conception must have occurred during an undetected extra-territorial foray by one or both animals.

Behavioural data suggested that bat-eared foxes have the potential to engage in extra-pair copulations without altering their usual ranging patterns. The identification of fm9 as an extra-pair father supports this suggestion. A number of other studies have demonstrated that neighbouring males are the most likely sires of extra-pair offspring. For example Roemer *et al.* (2001) identified a single male as the most likely father of extra-pair cubs of two neighbouring females (for an avian parallel see Yezerinac *et al.* 1995).

In some species of bird it has been shown that young males suffer more cuckoldry than old males (Bollinger & Gavin 1991), and that old (Wagner *et al.* 1996) or large (Kempenaers *et al.* 1992) males are most likely to be chosen as extra-pair mates, perhaps because age and size are indices of fitness (Wagner *et al.* 1996). While data from this study are obviously limited, it is worth noting that fm27 was a similar age to males fm9 and fm25 (based on toothwear), that all animals had previous (successful) breeding experience, and low ecto-parasite loads. Fm27 was, however, quite small in comparison to these other two animals (3.4 kg vs. 3.7 & 3.8 kg). Although the level of paternal assistance provided by fm27 was relatively low, it was not the lowest for any male (Figure 3.1).

Maas (1996) found that, in the Serengeti, bat-eared foxes regularly pair with 1st degree relatives. This has also been demonstrated in the Ethiopian wolf (Sillero *et al.* 1996), and

suggested to explain the prevalence of extra-pair copulations in the species. Further genetic analysis will reveal if this explains the extra-pair paternity observed in the Astra group (i.e. if fm27 & ff28 are closely related).

6.4.2 Why is extra-pair paternity infrequent in bat-eared foxes?

Behavioural data presented in section 5.4.1 demonstrate that some (2 of 4) females were as involved as their partners in maintaining close proximity during the mating season. This may reflect the fact that females paired to high quality males may have little or no interest in pursuing extra-pair copulations (see Kempenaers *et al.* 1995). However it is unlikely that this alone explains the low levels of EPP observed in this population, because a substantial portion of socially monogamous females are likely to be paired with sub-optimal partners (Gowaty 1996, Petrie & Kempenaers 1998). Additionally, some benefits females may accrue by mating with extra-pair males (e.g. increasing offspring variability) exist irrespective of the quality of their social partner.

Why then are levels of EPP so low in this population? Petrie and Kampenaers (1998) predict that levels of EPP are expected to vary according to benefits and costs to females, and constraints on female choice: -

Benefits to females

The indirect (genetic) benefits of engaging in extra-pair copulations are predicted to vary according to the degree of variation among males (Petrie & Lipsitch 1994). Where there

is little genetic variation between males, the benefits of having offspring sired by extra-pair males are likely to be reduced (whether females seek good genes or enhanced offspring variability). This hypothesis is backed up by data showing that, across bird species, levels of extra-pair paternity correlate with the proportion of polymorphic loci (Petrie *et al.* 1998).

Could lack of genetic variation among males provide an explanation for the low levels of EPP observed in this population? Mean levels of heterozygosity (across the 13 loci typed) were quite high (H=0.59, see Table 6.2), suggesting that substantial genetic variation existed among males. Certainly, levels of heterozygosity are higher than reported in the island fox (H=0.49, Roemer *et al.* 2001) a species that has lower levels of genetic diversity than it's mainland counterpart, the Gray fox (Wayne *et al.* 1991), and significantly higher levels of extra-pair paternity (25 %, Roemer *et al.* 2001; comparing proportion of extra-pair young in that study (4 of 16) with this study (2 of 44)- X^2=4.42, d.f.=1, $p<0.05$). Lack of variation among potential fathers thus does provide a likely explanation for the low levels of extra-pair paternity observed in this population.

Costs to females

The main cost to a female in seeking extra-pair copulations may be the loss of her partner's investment in her offspring (Birkhead & Moller 1992, section 3.1.4). In bat-eared foxes the potential cost of reduced male investment is high, because male care enhances reproductive success (chapter 3). However, because males are only expected to

adjust levels of care under certain conditions (section 3.1.4), it is uncertain whether this cost exists for female bat-eared foxes. Males are not expected to reduce levels of care unless this increases future reproductive success (Maynard Smith 1977). As females are not in estrus during the period of cub rearing, reduction in male care would not result in increased mating opportunities. Having said this, because male care is likely to carry a substantial energetic cost (section 3.4.4), reduction in care could increase male survival. More (preferably experimental) data (see Sheldon 2002) are required to investigate the possibility that canid males might facultatively adjust levels of care according to their confidence of paternity.

The costs of engaging in extra-pair copulations are also expected to vary according to species ecology. If the energetic costs of extra-pair prospecting and mating are greater than any potential benefits, the behaviour should not be favoured. Stanback *et al.* (2000) have suggested that this cost could explain the absence of extra-pair paternity in the desert living Monteiro's hornbill (see also Lawless *et al.* 1997). Data on bat-eared fox activity budgets (Table 5.3.3) show that females spend the vast majority of the night actively foraging. This suggests that the energetic costs of engaging in alternative activities, such as extra-territorial prospecting, would be high (particularly as lactating females may rely on fat reserves gained prior to parturition, section 3.4.3). For the same reasons extra-territorial prospecting will also be energetically costly for males.

Constraints on female choice

The ability of females to engage in extra-pair copulations will depend on how well their partners are capable of guarding them, which is itself affected by the degree to which mate guarding interferes with normal foraging behaviour. If mate guarding reduces foraging efficiency males will face a trade-off between the two activities, and males may be incapable of defending females throughout their fertile period (e.g. Komdeur 2001). This is illustrated well by an experimental study of red-winged black birds showing that males provided with supplementary food spent less time foraging, more time guarding their partners and gained higher levels of paternity (Westneat 1994).

Data presented in chapter 5 demonstrate that the ecological constraints on male mate guarding are likely to be minimal in bat-eared foxes. The maintenance of close partner proximity does not appear to reduce feeding rate (section 5.3.3), suggesting that males do not face a trade-off between mate guarding and foraging. As a result, it may be relatively easy for males to maintain close proximity with their partners throughout their fertile periods. This is further supported by the observation that males stayed very close to their partners throughout the breeding season (section 5.3.1). This suggests that paired males are likely to be in a strong position to prevent their partners from engaging in extra-pair copulations, and that male behaviour places a considerable constraint on female mating options.

Other factors potentially restricting extra-pair mating

Several avian studies have demonstrated that levels of extra-pair paternity increase with population density, apparently because it becomes easier for individuals to assess extra-pair mates and engage in extra-pair copulations (e.g. Gowaty & Bridges 1991). Roemer at al. (2001) have suggested that high population density may partly explain the high levels of extra-pair paternity observed in the island fox. Although bat-eared foxes have been reported living at higher densities elsewhere (see section 4.4.1), it seems unlikely that low population densities prevented bat-eared foxes on the study site from engaging in extra-pair mating, because the ranges of neighbouring animals often overlapped considerably, and foxes were often found 'interacting' with neighbours (chapter 5).

Levels of extra-pair paternity may also vary according to the degree to which breeding is synchronized. If breeding is highly synchronized it can be difficult for males to simultaneously guard their partners and seek extra-pair copulations (Weatherhead 1997). It seems unlikely that this factor alone explains the low levels of extra-pair paternity in the population, because although breeding was synchronized (Table 4.5), a good proportion of males apparently had the opportunity to guard their own mates (for extended periods) and seek extra-pair matings with other females on the study site (Figure 4.3).

6.4.3 summary

Bat-eared foxes on the study site were shown to be predominantly genetically monogamous. A number of factors probably operate to prevent extra-pair copulations (and paternity) occurring on more than an irregular basis: -

Perhaps the primary factor promoting mating fidelity in the species is the fact that it is relatively easy for males to maintain close proximity with their partners during the breeding season. In fact, even outside of the breeding season, the behaviour of mated partners is usually highly co-ordinated (section 4.3.1). Because of this, it is likely to be very difficult for females to engage in extra-pair copulations. Even if females could achieve some extra-pair matings, it is likely that their partners could detect this, and possibly respond by reducing levels of paternal investment.

This scenario probably explains why male bat-eared foxes, unlike males of some other fox species, do not adopt a roaming strategy during the mating season. Because males can probably prevent their partners from gaining uninterrupted access to other mates, the chances of achieving extra-pair copulations are likely to be slim. Combined with a likely high energetic cost of extra territorial prospecting, it seems likely that, even for the most competitive males, the costs of a roaming strategy would outweigh any potential benefits.

Chapter 7

General Discussion

7.1 Aims of Chapter

The purpose of this chapter is to review the data presented in this thesis, and to summarize and discuss conclusions regarding: -

1) The factors favouring the maintenance of social monogamy in the bat–eared fox, and other species of canid.
2) Whether and why bat-eared foxes, and other species of canid, mate outside the pair bond.
3) The factors that favoured the origin of the pair bond and social monogamy in ancestral canids.

7.2 The maintenance of social monogamy in the bat-eared fox

7.2.1 The adaptive significance of male care, and its effect on male mating options

One of the major aims of this study was to identify the extent to which paternal care enhances offspring survival, and the effect this has on male and female mating options. Like previous studies of the species (Lamprecht 1979, Malcolm 1986, Maas 1992, Pauw 2002), I found that bat-eared fox males play a special role in the care of offspring. During

the first 14 weeks of cub life, males are primarily responsible for their direct care, guarding, grooming, provisioning and accompanying cubs on foraging trips (see box 3.1). Females, by contrast, spend the vast majority of this time away from the den foraging (section 3.4.1).

Data presented in the thesis demonstrate that female bat-eared foxes invest very heavily in reproduction, feeding at close to maximum rate throughout gestation and lactation, and suffering increased mortality during lactation (section 3.4.3). Unlike Moehlman (1986), however, I suggest that this is unlikely to decrease or remove the requirement for male care. Time constraints associated with termite eating dictate that lactating females have very little time available to spent at dens (section 3.3.3), and this seems to make male involvement in direct cub care all the more important. This conclusion is supported by the fact that male attendance at breeding dens significantly correlated with cub survival (section 3.4.4), and the observation that widowed (lactating) females adjusted their behaviour in order to spend more time at dens (Maas 1993, section 3.3.2).

Given that male care does enhance offspring survival, is it likely that males could increase their reproductive success by dividing their care between the litters of multiple females, or does the requirement for paternal care constrain males into being monogamous?

The answer to this question is somewhat a matter of speculation. However, given of the extent to which male care enhances offspring survival, the fact that substantial variation

in the expression of male care existed (such that some males spent more than twice as much time with cubs than others, section 3.3.1), and the observation that females can sometimes succeed in rearing cubs without male assistance (Maas 1993), it is possible that under some circumstances polygynous males could rear more offspring than monogamous males (section 3.4.5). Certainly, if females coordinated their behaviour, and gave birth in a communal den, polygynous males would be very likely to gain increased reproductive success (a conclusion supported by Maas' (1993) observation of polygynous groups in the Serengeti).

7.2.2 Costs of polygyny for females

There are several ways in which polygyny can potentially reduce female reproductive success (Bensch 1997). The two most important of these result from the costs of sharing beneficial male care (Davies 1992), and the costs of sharing a territory and access to food (Orians 1969, Davies 1989).

Because male care increases cub survival, and breeding is synchronized (so males could not provide care for multiple litters sequentially), it seems highly likely that polygnous females would suffer a significant cost by sharing male care. This cost would be greatest for females breeding in separate dens, but would also exist for females breeding in a communal den, because some forms of care males provide, like grooming, provisioning and transporting cubs are depreciable (see Kleiman & Malcolm 1981).

Would polygyny be likely to substantially reduce females access to food? For insectivorous species, high prey renewal rates can reduce the cost of sharing a territory (Waser 1981, chapter 4), and favour communal foraging (Davies & Houston 1984). In accordance with this, Lamprecht (1979) and Malcolm (1986) have both suggested that bat-eared foxes do not suffer the usual costs of group living associated with competition over food, and proposed that grouping could even enhance the ability of foxes to utilize their insect prey (and possibly detect predators). Maas (1993 p.106), on the other hand, states that there could still be a residual cost to communal foraging.

In this study, evidence regarding the likely effect of polygyny on female access to resources was mixed. On one hand, some territories appeared to contain more than enough food to support an additional breeding female (section 4.3.5), and groups of more than 2 animals (adults with fully grown cubs) regularly foraged in close proximity without this appearing to reduce their feeding rate (appendix 3.6- although the feeding rate of group feeding foxes was not quantified or compared with that of foxes foraging singly or in pairs). On the other hand access to resources appeared critical for successful reproduction, as territory quality (and size) significantly correlated with several measures of reproductive success, and females on small territories had a greater chance of dying during lactation (chapter 3). More data are required to fully investigate this issue.

Another possible cost to polygynous females sharing a communal den would result from their cubs' competing for access to milk. This cost is likely to exist in bat-eared foxes,

because polygynous females observed by Maas (1993) suckled each other's cubs indiscriminately, but did not suckle at the same time. The costs of inter-litter competition at the teat have been demonstrated in a number of species where females nurse offspring communally (e.g. Mennella *et al.* 1990).

In summary, it seems certain that polygynous females would suffer a cost by sharing male care, likely that they would suffer the cost of inter-litter competition at the teat, and possible that they would suffer the cost of reduced access to resources. Data from Maas (1992), while not identifying the cause of the reduction, demonstrated that polygynous bat-eared fox females did suffer reduced reproductive success. Because of this, it is likely that resident females would always gain by excluding unrelated females from their territories, and that, under most circumstances, un-mated females should avoid being recruited into polygynous groups.

7.2.3 What prevents males from becoming polygynous

Assuming that males could gain from defending multiple dispersed females, what factors prevent them from doing so?

As discussed in the previous section, females probably have an interest in promoting monogamy, and it is likely that they are in a strong position to prevent polygyny occurring. Unmated females could readily detect the status of 'paired' males, and avoid mating with them (section 4.4.5), and paired females could probably exclude additional

females from their ranges, or at least prevent them from breeding (e.g. see Macdonald 1979, 1980).

Could males become polygynous by defending the (exclusive) ranges of more than one female (Clutton-Brock 1989)? Data on female spatial distribution and breeding synchrony suggest that it would be difficult for males to court multiple dispersed mates, particularly if a prolonged period of mate guarding is required to ensure paternity (section 4.3.6). Added to this intense male competition for mates (section 4.3.7), and it seems likely that attempted polygynists would have more chance of loosing their original partners (section 4.4.5) than they would of gaining additional mates.

While is not clear whether females employ behavioural strategies that prevent polygyny occurring (beyond seeking to occupy largely exclusive ranges), it seems very likely that polygyny could only a viable male strategy if females were willing to share a territory and co-ordinate their behaviour to some degree. This conclusion is consistent with the observations of Maas (1993), who found that polygyny only occurred when related females shared a territory and communal den. It also emphasizes the fact that females often play a key role in shaping mating and social behaviour (see Ahnesjo *et al.* 1993).

7.2.4 Why does polygyny occasionally occur in bat-eared foxes

Given that polygynous females compete for male care and potentially for food, and that they suffer reduced reproductive success (Maas 1993), why does polygyny ever occur in bat-eared foxes?

In a number of canid species offspring sometimes delay dispersal and remain on their parents' territory during a subsequent breeding season. In most species these 'philopatric' offspring act as non-breeding 'helpers' (red foxes- Macdonald 1979, black-backed and golden jackals- Moehlman 1989, swift foxes- Kitchen *et al.* 1999, crab-eating zorros- Macdonald & Courtenay 1996, arctic foxes- Strand *et al.* 2000), although subordinate females may occasionally breed (see next section). Although helpers exhibit the apparently paradoxical behaviour of forsaking breeding (Emlen 1991), it is likely that the benenfits of staying and helping outweigh the high costs of dispersal (Jennions & Macdonald 1994). Philopatric offspring can gain a number of benefits, including increasing the production of non-descendant kin (after Hamilton 1964, see Macdonald 1979, Moehlman 1989) and increasing their chance of eventually gaining a breeding territory (Maas 1993).

Bat-eared foxes differ from most other canid species in that philopatric daughters routinely breed, sharing a communal den with their mothers (Maas 1993, Pauw 2000). The fact that philopatric daughters breed, rather than act as helpers, probably relates to the species insectivorous diet (Maas 1993). Because termites cannot readily be carried

back to the den in any form other than milk, there is little scope for non-breeding helpers to assist their parents. Additionally, because of the low cost of sharing insect prey (section 7.2.4), competition for food between breeding females is likely to be low (at least relative to other canids- Maas 1993). Although the number of offspring raised by each female may be reduced, when opportunities for dispersal are limited it is likely that mothers and daughters can both increase their inclusive fitness (sensu Hamilton 1964) by breeding in breeding in polygynous groups (Maas 1993, see also Cant & Johnstone 1999).

7.2.5 The maintenance of social monogamy in other canid species

It seems likely that the factors promoting monogamy in bat-eared foxes operate to promote monogamy in other species of small and medium sized canid: -

The fact that most canid males provide significant assistance to females during reproduction (section 3.1.2) suggests that polygynous females would again suffer by sharing paternal care. Indeed, the costs of sharing male care may generally be greater in other canid species, because males are generally more involved in the provisioning of females and offspring (the most 'depreciable' form of male care). The costs of polygyny associated with sharing access to food are also likely to be greater in other species of canid, because 'prey' renewal rates are likely to be substantially lower than they are for the insectivorous bat-eared fox.

Both of these facts suggest that females of most canid species, probably to a greater extent than bat-eared foxes, will have an interest in avoiding polygyny. Because of the facts that unrelated female canids tend to occupy exclusive ranges and have restricted breeding seasons (section 4.1.4), it again seems likely that polygyny will only be a viable male strategy if females were willing to co-ordinate their behaviour, at least to the extent that they occupy a joint or largely shared range.This conclusion is once more supported by the fact that that polygyny most often (though perhaps not only) occurs when female offspring breed on their natal territories, denning either separately or in a communal den with their mothers (in red foxes- Macdonald 1979, Zabel & Taggart 1989; in arctic foxes- Strand *et al.* 2000).

7.3 The mating behaviour of bat-eared foxes and other monogamous canids

7.3.1 Explaining the low levels of extra-pair paternity observed in this population of bat-eared foxes

A major aim of this research project was to establish if and why bat-eared foxes mate outside of the pair bond. In doing so we hoped to shed light on the factors that shape the mating behaviour of canids, and other species of socially monogamous mammal.

Genetic data presented in chapter 6 revealed low levels of extra-pair paternity among bat-eared foxes on the study site. Out of 44 offspring tested, only 2 (or 4.5 %) were unlikely to have been sired by their social father. Like other aspects of bat-eared fox social

behaviour, I suggest that the low levels of extra-pair paternity may be partly related to the species insectivorous diet: -

Bat-eared fox partners maintained extremely close proximity during the mating period, and often foraged together at other times of year (section 5.3.1). Because the maintenance of close proximity does not appear to reduce foraging efficiency (see section 5.3.3), bat-eared fox males (and females) do not appear to face a trade-off between mate guarding and foraging (c.p. Weatherhead 1995 & Komdeur 2001). As a consequence, it is likely to be relatively easy for males to remain close to their partners during the mating season, and to prevent them from gaining uninterrupted access to other mates.

Time budgets associated with termite eating diet also dictate that adult foxes have little 'spare time' for engaging in alternative activities (section 5.3.3). Searching widely for additional mates would therefore be likely to interfere with feeding, and exact a high energetic cost (section 5.3.3, see also Palokangas *et al.* 1993). Combined with the fact that oestrous females are likely to be effectively guarded by their partners (see above) it seems likely that, even for the most competitive males, the costs of roaming widely in pursuit of extra-pair copulations would exceed any potential benefits. This conclusion is consistent with the observation that neither males nor females adjusted their range sizes or travelling speeds during the mating season (section 5.3.5).

On the other hand, there are reasons why extra-pair mating (and paternity) may occasionally occur. Bat-eared fox home ranges regularly overlap with those of their

neighbours (section 4.4.3), and neighbouring animals interact more than would be expected by chance (section 5.3.6). Because of this foxes may be able to assess potential extra-pair partners and occasionally engage in extra-pair copulations without altering their usual ranging patterns. This is suggested by the fact that one neighbouring male was identified as a potential sire of one of the two extra-pair cubs (section 6.4.1). The home range of this male overlapped considerably with that of the cub's mother (and father), and these animals were found 'interacting' during the run-up to the mating season.

7.3.2 Mating behaviour of other canid species

As was discussed in section 5.1.4, there is evidence that male of some fox species roam widely during the mating season (red fox, kit fox, island fox), whereas males of other species do not appear to do so (blanfords fox, bat-eared fox). If the function of this roaming behaviour is the pursuit of extra-pair copulations, levels of extra-pair paternity may be lower or absent in species where males do not roam. This prediction is consistent with genetic data so far available, with this study showing low levels of extra-pair paternity, Roemer *et al.* (2001) showing moderate levels of EPP in the island fox, and unpublished data from an urban red fox population revealing extremely high (>50%) levels of extra-pair paternity (Philip Baker, personal communication).

So while the social systems of small canids may be superficially similar, there appears to be considerable variation in their mating behaviour. What factors are likely to underpin this variation? The mating strategy individuals of a particular species adopt presumably

depends on the costs and benefits of pursuing extra-pair copulations. These may vary according to a number of factors, including the degree to which the behaviour of mated partners is synchronized (see previous section), time and energy constraints imposed by diet (see previous section), levels of breeding synchrony in the population (see section 4.3.6), and the degree to which females rely on paternal care. Assessment of the relative importance of these factors will require behavioural and genetic data from a wider range of canid species.

An additional demographic factor that may promote a roaming strategy in some species of fox is that there may be a substantial population of 'un-paired subordinates' routinely available for mating. Zabel & Taggart (1989) suggest that many female red foxes mate as subordinates, but only carry young to parturition or succeed in rearing young when ample food resources allow them to do so. This strategy could be promoted if there is difficulty of predicting food availability at the time of mating, given that the costs of gestation are typically much lower than those of lactation (Clutton-Brock 1991). The fact that prenatal loss in red foxes is high, having been estimated at between 12-36% (Layne & McKeon 1956, Englund 1970), supports this suggestion. If subordinate mating favours roaming we would expect wayfaring behaviour to be associated with subordinate mating, between populations and species.

7.4 The evolution of the canid pair bond

The basic canid social unit consists of a long-lived pair bond, where males are involved in the care of young and the pair continues to interact between breeding seasons (Asa & Valdespino 1998). The fact that the pair bond and the expression of paternal care are traits common to the majority of modern canids suggests that both evolved in a now extinct ancestor (Kleiman & Eisenberg 1973). Because it is impossible to know the social and ecological pressures that acted on this ancestral species, conclusions regarding the origins of the canid pair bond are necessarily speculative. However, data presented in this thesis and elsewhere can be used to develop a 'most-likely evolutionary scenario' of how bi-parental care and social monogamy came to evolve and predominate among the canids.

There are good reasons for believing that the canid pair bond is unlikely to have evolved from an ancestral mating system in which male care was required or expressed. Firstly, the requirement for paternal care is unlikely to have evolved prior to its expression, because this would lead to females suffering an unnecessary cost (Dunbar 1995- see section 4.1.1). Secondly, because there are very few non-monogamous species of carnivore (or mammals in general) in which males help rear offspring, it seems unlikely that the canid pair bond evolved from a mating system in which paternal care was already expressed (a conclusion is supported by the analysis of Komers & Brotherton 1997). If this is the case, it is also unlikely that females had the same (or possibly any) interest in promoting monogamy. Why then did the canid pair bond originally evolve?

The fossil record suggests that the canids evolved in North America, and that ancestral forms were unspecialised animals, similar to modern day gray foxes (Kurten 1971, Martin 1989). Because of the probable omnivorous diet of these animals, it is likely that their 'prey' was sparse and evenly dispersed, and therefore that females occupied largely exclusive ranges (as do the females of the vast majority of small carnivore species e.g. Sandell 1989, see also Wright 1984, 1986). Because these animals lived in a seasonal environment, it is also very likely that they had restricted annual breeding seasons.

Data presented in this thesis suggest that the above combination of factors (alone) make it difficult for male to monopolize multiple females (chapter 4, Emlen & Oring 1977). It is clear, however, that this combination of factors does not necessarily lead to the evolution of social monogamy. For example, among the Mustelidae (stoats, weasels and otters), females occupy largely exclusive ranges and breeding is seasonal, but most males adopt a roaming strategy during the mating season, visiting and mating with as many oestrous females as possible (e.g. Sandell 1986). Similarly, among the Viverridae (genets, civets and mongooses), the same combination of factors often leads to males continuously defending the ranges of several females (e.g. Palomares 1993). Are there additional or different selective forces acting on canids that can explain these differences?

One potential explanation for these differences lies with the fact that canid females are mono-estrous spontaneous ovulators, with well-advertised oestrous periods (Asa & Valdespino 1998, whereas female felids, mustelids and viverrids are poly-oestrous

induced ovulators). While we cannot be certain that these reproductive features evolved prior to the pair-bond, it is likely that they promote prolonged mate-guarding (section 4.1.7), and reduce the ability of males to monopolise multiple females (section 4.3.6).

The evolution of monogamy in canids could also be related to diet. Because canids are generally more omnivorous than other species of carnivore, they may generally be required to spend a greater proportion of their time foraging. This may place a constraint on the amount of time males have available to 'roam' during the mating season, or invest in the defence of more than one female. At the same time, because food renewal rates may generally be higher for omnivorous species (relative to strict carnivores), the costs of sharing an entire foraging range with another animal (as socially monogamous species tend to do) are likely to be reduced (Waser 1981).

In conlcusion, because ancestral female canids are likely to have occupied exclusive ranges and had restricted annual breeding seasons, it is likely to have been difficult for males to monopolise females. Add to this the potential requirement for a prolonged period of mate guarding (related to female oestrus), and high energetic costs of attempting to monopolise multiple females (related to diet), and it seems likely that the costs of being polygynous (a reduced ability for a male to defend his 1st mate and territory, and/or an increase in energetic expenditure and predation risk, see Kishomoto & Kawamichi 1996, FitzGibbon 1997) would be likely to outweigh any potential benefits (the possibility of fertilizing more than one female per breeding season). I propose that the canid pair bond probably evolved for these reasons, and that that expression (and

requirement) for male care is likely to have developed shortly after the evolution of the pair bond.

7.5 Suggestions for future work

The most fruitful approach to further investigation into why bat-eared foxes and other small canids usually breed in socially monogamous pairs may be through detailed examination of the circumstances under which polygyny occasionally occurs:

It will be informative to determine whether polygyny always involves co-operation between related females, or if males are sometimes able to defend multiple females whose behaviour is not co-ordinated. When polygyny occurs through female co-operation, as it sometimes does in the bat-eared fox (Mass 1993), it would be useful to examine the costs that polygynous females incur relative to monogamous females (see section 7.2.2). This will allow assessment of why females are usually unwilling to form such groups. If males are occasionally able to attain polygynous status by defending the territories of non co-operative females, it will be interesting to determine the ecological circumstances under which this occurs. This would again allow assessment of why social monogamy usually predominates.

More detailed ecological studies of lesser known small canid species will shed light on whether the requirement for male care is a critical factor favouring social monogamy. If there are species in which social monogamy persists in the absence of a requirement for

male care (as, for example, may for example be the case in Blanford's fox- Geffen & Macdonald 1992), this would clearly indicate that other factors prevent polygyny from occurring.

Another area requiring future research is to establish whether 'socially polygynous' canid groups are genetically polygynous. If polygyny usually occurs when daughters breed on their natal territories, it would be somewhat surprising if these females mated with the group male, as he would probably be their genetic father. It could be that polygynous groups, rather than representing instances in which males can successfully defend multiple females, represent instances in which dominant pairs permit related females to breed on their territories. If close inbreeding does occur in small canid species (as Maas 1993 suggests may be the case in the bat-eared fox) it will be fascinating to investigate how natural selection can favour this behaviour. Addressing these questions will require genetic data from polygynous breeding populations.

Available genetic data suggests that there is real variation in the extent to which socially monogamous canids are genetically monogamous (see section 7.3). Identifying the factors that underpin this variation will require genetic and behavioural data from a wider variety of canid species. If, for example, the high levels of genetic monogamy in bat-eared foxes are favoured by the highly co-ordinated behaviour of mated partners, we would predict that species with similarly behaviour (e.g. the crab-eating fox, Macdonald & Courtenay 1996) to show high levels of genetic monogamy.

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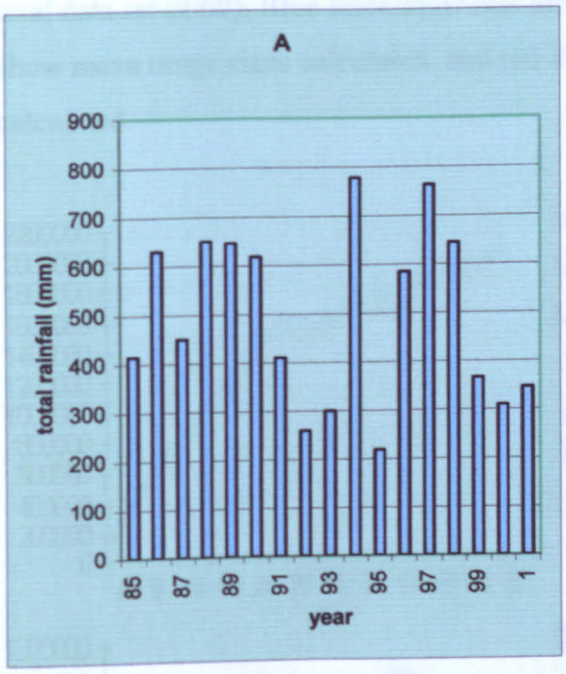
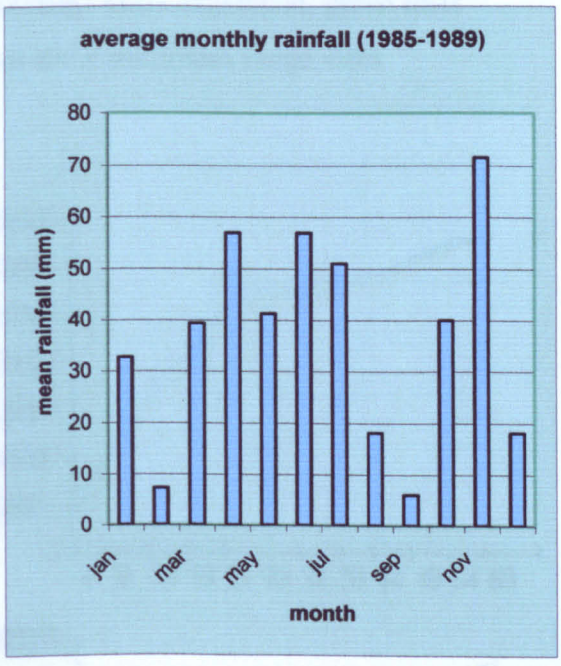
Appendices

Appendix 2.1 Rainfall on the study site

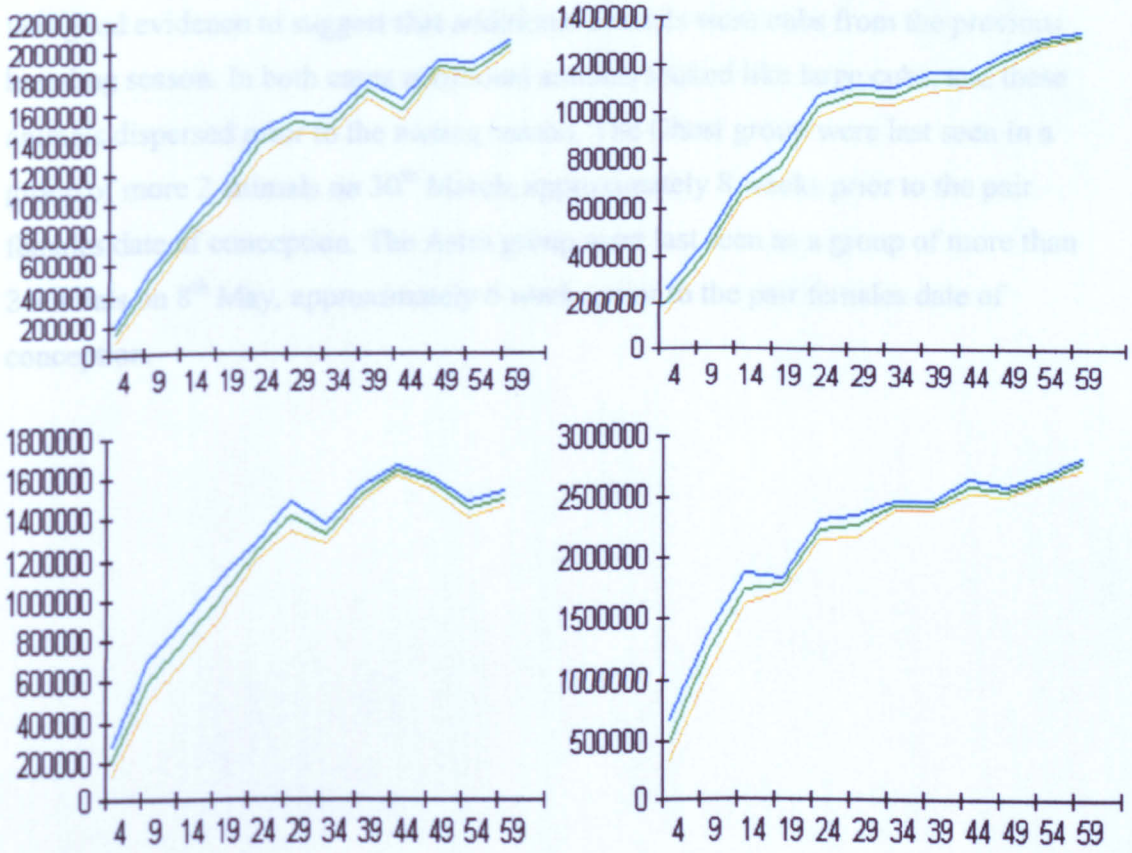
The two graphs below show annual rainfall of the study site between 1985 and 2001 (left), and average monthly rainfall on the study site between 1985 and 1989 (right).





Appendix 2.2 Evidence that 60 radio-tracking fixes provided a reasonable estimate of home range size

The 4 graphs shown below show how Minimum Convex Polygon home range sizes increased with the number of radio-tracking fixes used (for 4 randomly chosen foxes). Range sizes were calculated at 5 fix intervals, and for each 'fix number' 10 MCP ranges were calculated (from a randomly chosen combination of fixes in a total data set of 60). Blue lines show maximum range sizes calculated, green lines show mean range sizes calculated, and red lines show minimum range sizes calculated.



Appendix 3.1 Evidence that foxes on the study site lived in pairs

Table 3.1 (overleaf) shows that, with the exception of the Astra and Ghost groups, during the 6 month run-up to the 2001 breeding season all groups of foxes on the study site were encountered most often in pairs. This was particularly true during the day, when foxes were always found resting under bushes with their partners (usually in bodily contact). Only in the Camp and Mzee groups were adults found resting alone during the day, and this occurred only once for each of these groups. In no cases were foxes observed actively foraging.

The Astra and Ghost families were found in groups of up to 4 animals, but there was good evidence to suggest that additional animals were cubs from the previous breeding season. In both cases additional animals looked like large cubs, and these animals dispersed prior to the mating season. The Ghost group were last seen in a group of more 2 animals on 30th March, approximately 8 weeks prior to the pair females date of conception. The Astra group were last seen as a group of more than 2 animals on 8th May, approximately 6 weeks prior to the pair females date of conception.

Table 3.1 Number of individual foxes seen when the 10 study groups were sighted in the 6 months leading up to parturition in 2001.

	number of animals seen							
	day				night			
group	1	2	3	4	1	2	3	4
camp	1	4	0	0	4	5	0	0
everest	0	5	0	0	1	9	0	0
snorer	0	7	0	0	1	14	0	0
puffadder	0	7	0	0	0	5	0	0
junction	0	8	0	0	3	10	0	0
mzee	1	5	0	0	1	7	0	0
astra	0	3	1	2	4	15	0	1
ghost	0	3	2	1	2	6	1	1
neil	0	4	0	0	0	1	0	0
grebe	0	3	0	0	1	2	0	0

Appendix 3.2 Diurnal behaviour and den attendance of adults with cubs under 14 weeks of age.

During the 2001 breeding season, I collected data on the diurnal behaviour of adult foxes with pre-weaned cubs. The purpose of these data was to establish the parental roles of males and females during daylight hours, and confirm that no more than two adults were involved in any breeding attempts. A total of 90 observations were made from 10 breeding fox-pairs (see Table 3.2 overleaf).

Mated partners were almost always found together (on 85/90 observations from all groups), although sometimes one adult was inside the den while the other rested at or near the den entrance. On no occasions were more than 2 adults observed at or near breeding dens, strongly suggesting that foxes on the study site bred only in socially monogamous pairs. Data on behaviour is not presented because during all (90) observations foxes were found resting. Although these data were not collected shortly after sunrise or shortly before sunset, they confirm that during the breeding season, as during the non-breeding season (appendix 3.1), foxes are inactive for at least the majority of the day.

Table 3.2 Diurnal proximities of 10 pairs of foxes with pre-weaned pups to breeding dens. The table shows the number of times foxes were found at given distances from their dens. Numbers in parenthesis are numbers of observations made for each cub age class.

			Distance from den			
Group	*Sex*	*N*	inside den	0-10m	10-50m	50m +
Ghost	M	9 (0,1,1,2,1,2,2)	0	3	0	6
	F	as above	1	2	0	6
Puffadder	M	9 (1,0,2,1,1,2,2)	5	4	0	0
	F	8 (0,0,2,1,1,2,2)	3	5	0	0
Snorer	M	11 (2,1,3,2,1,0,2)	2	6	3	0
	F	as above	3	5	3	0
Astra	M	11 (2,1,2,2,2,1,1)	2	8	1	0
	F	as above	4	7	0	0
Neil	M	12 (2,3,1,2,2,1,2)	5	6	0	1
	F	as above	7	4	0	1
Mzee	M	11 (1,3,3,2,2)	6	3	0	2
	F	as above	9	2	0	0
What	M	7 (0,2,1,1,0,2,1)	2	4	0	1
	F	as above	3	4	0	0
Grebe	M	5 (2,1,1,1,0,0,0)	4	1	0	0
	F	as above	5	0	0	0
Junction	M	5 (1,1,1,1,0,0,1)	1	2	1	1
	F	as above	2	2	1	0
Camp	M	2 (2,0,0,0,0,0,0)	0	2	0	0
	F	as above	1	1	0	0

Appendix 3.4 Proximity of lactating females to breeding dens

Table 3.4 (overleaf) presents data on the proximity of lactating females to breeding dens. Two of the three females, ff28 & ff29, spent very little time close to their breeding dens. These females were found within 100 m of dens on only 2 of 45 or 4.4% of observations, and only ff28 was seen at the den (once). Both of these females were found further than 300m from dens on approximately 80 % of fixes. In comparison, female ff16 spent one third of time within 100m of the den (on 10 of 15 of these fixes the female was at the den entrance), and approximately 55 % of the time more than 300m from it's den.

For two females, estimates of den proximity differed significantly from the estimates based on radio-tracking data (comparing data from same individuals from the same year; ff16- X^2=9.83, d.f.=4, $p<0.05$, ff28- X^2=13.1, d.f.=4, $p<0.01$), and for one female they did not (ff29- X^2=5.9, d.f.=4, N.S.). However, combining data from these females, estimates did not differ from combined radio-tracking data for these (X^2=3.57, d.f.=4, N.S.) or for all females (X^2=8.64, d.f.=4, N.S.).

Table 3.4 Distances of 3 lactating females to breeding dens. Each female was followed 3 times, once during each time slot (pup age at each follow is also given). Proximities are expressed as total number of and % (in parenthesis) of observations within given separation distances.

Group	ID	pup ages	distance from den 0-100m	1-200m	2-300m	3-400m	400m+
Astra	ff28	5,7,10	2 (4.4)	6 (13.3)	2 (4.4)	10 (22.2)	25 (55.6)
Junction	ff29	4,7,10	2 (4.4)	1 (2.2)	5 (11.1)	1 (2.2)	36 (80)
Snorer	ff16	6,8,11	15 (33.3)	4 (8.8)	1 (2.2)	3 (6.7)	22 (48.9)
		$\bar{x}$	14.0	8.1	5.9	10.4	61.5
		S.D.	16.7	5.6	4.6	10.5	16.4

Appendix 3.5 Evidence for direct provisioning of cubs by adults

During 2001 & 2002, fox den sites were inspected for evidence of direct provisioning of cubs. The following observations confirm that at least some direct provisioning of cubs occurred, with small birds, small mammals and large insects being found inside den entrances or next to dens: -

1) Pieces of chewed blooded bird feather (probably Mirafra spp.) found at entrance to Astra den on 13/09/02.
2) Feathers of similar bird species found in entrance to What den on 11/10/02, some of which had been chewed.
3) On 28/10/02 found a small shrew partially chewed at Ghost den.
5) At Puffadder den in 2001, found what was apparently the leg of a young hare, as well as a nightjar (Caprimulgus spp.) wing.
6) At several den sites, the remains of large insects, both grasshoppers and beetles, were found.

Appendix 3.6 Parental care and group cohesion after cubs were weaned

During the 2001 breeding season, 59 diurnal and 58 nocturnal sightings of bat-eared fox families were made between weaning and dispersal of cubs. These observations reveal that, during this period, parents and cubs are usually found in close association: -

On 44 of 59 (or 74.6 %) of day sightings all family members were found resting together. Adult pairs were found resting without pups on only 4 of 59 (or 6.8 %) of sightings. During the remaining 11 (or 18.6 % of) sightings, adults pairs were found with some (but not all) pups on 6 (10.2 % of) occasions, single adults were found with all pups on 2 (3.4 % of) occasions, and single adults were found with at some of their pups on 3 (5.1 % of) occasions. By the time pups reach 14 weeks of age

they became less reliant on dens. Only on 6 of 56 (or 10.7 %) daytime observations were pups found inside dens. The majority of the time groups rested in long grass or under bushes.

On 31 of 58 (or 53.4 %) of nocturnal sightings all family members were found together (could be sighted from the same location). Adult pairs were found without any pups on only 4 of 58 (or 6.9 %) of sightings. During the remaining 23 (or 39.7 % of) sightings, adults pairs were found with some (but not all) pups on 6 (10.3 % of) occasions, single adults were found with all pups on 6 (10.3 % of) occasions, and single adults were found with at some of their pups on 3 (5.2 % of) occasions and single adults were seen alone on 8 (13.8 % of) occasions. Males and females did not differ in the proportion of time that during which they were found with all (X^2=0, d.f.=1, N.S.) or some (X^2=0.11, d.f.=1, N.S.) of their pups.

On 46 of 48 nocturnal observations in which pups were seen, groups were actively foraging. Group members usually maintained close proximity while foraging; on 40 of 44 (90.0% of) observations when groups of 3 or more foxes were sighted, at least 3 foxes were found foraging within a hypothetical circle of 15m diameter. And on 35 of 44 (79.5% of) observations all foxes present were found foraging within a hypothetical circle of 15m diameter.

Appendix 4.1 Evidence suggesting that neighbouring fox pairs contained related individuals

During the course of the project, a number of incidental observations were made suggesting that neighbouring groups of foxes contained related individuals. These observations principally involved 'unusual' degrees social contact between 5 'pairs' of neighbouring groups; -

1) During March and April of 2001 the Juction and Mzee pairs were twice found resting together under the same small bush (during daylight hours).

2) The Astra and Ghost pairs were once found resting approximately 20m apart during the day. Additionally, during the 2001 breeding season, the lactating females from these groups were found foraging together 3 times.
3) The female from the Grebe pair was found resting with the neighbouring Ghost pair on 2 occasions during October 2001. Based on this animals tooth-wear, it appeared to be younger than either member of the Ghost pair.
4) The female from the Airstrip group (ff62), a group that took over the Grebe territory, joined the neighbouring Ghost pair after the death of her partner and the assumed death of her cubs. Judging on tooth-wear, this female was again younger than either member of the Ghost pair.
5) The What and Neil's groups, 2 groups with a high degree of range overlap, used one of the same breeding dens (though not simultaneously) during the course of the 2001 breeding season.

Taken together this evidence suggests that young foxes (in most of these cases females) may pair up and establish territories next to those of their parents. It is not clear if neighbouring pairs with high degrees of range overlap always contain related animals (e.g. on my study site there was no behavioural evidence suggesting relatedness between the snorer and puffadder groups). Genetic data will shed more light on this possibility.